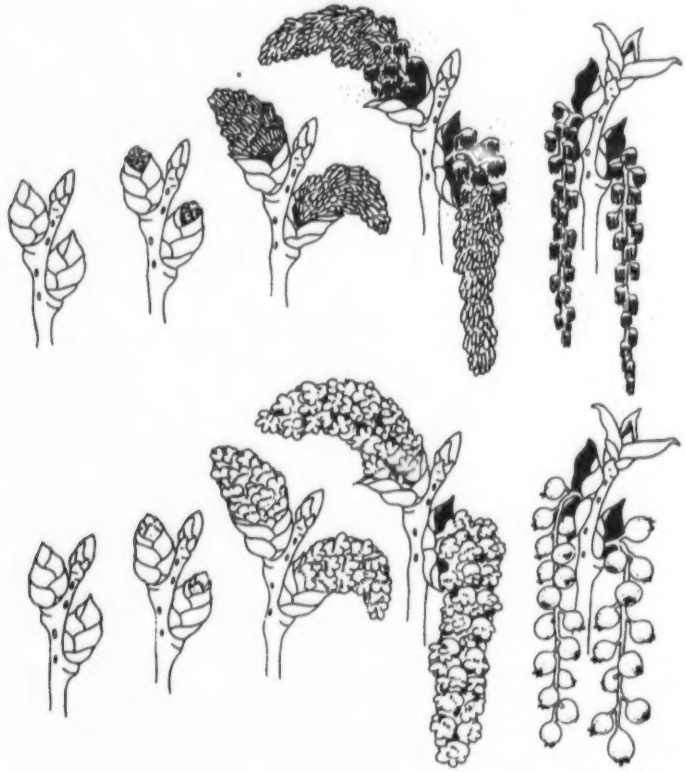
Final Report for
Alberta Environmental Protection
Contract #97-0126

OLDMAN RIVER BASIN - RIPARIAN COTTONWOODS

March 1997



male (top) and female (bottom) cottonwood catkin development

submitted to: **John Mahoney**, Project Biologist,
Oldman River Dam, Alberta Environmental Protection,
Pincher Creek, Alberta T0K 1W0

by: **Lori A. Gom, Andrea R. Kalischuk, Jennifer Willms, Walter Willms, Mel Tyree, and Stewart B. Rood**
Department of Biological Sciences, University of Lethbridge,
Lethbridge, Alberta T1K 3M4

Final Report for
Alberta Environmental Protection
Contract #97-0126

OLDMAN RIVER BASIN - RIPARIAN COTTONWOODS

March 1997

Table of Contents:

Table of Contents 1

Summary 2

1. Characterizing the clonal composition of a cottonwood grove in southern Alberta according to morphology and phenology;
by: L.A. Gom and S.B. Rood 4

2. Branch growth of riparian cottonwoods:
A hydrologically sensitive dendrochronological tool;
by: J. Willms, S.B. Rood, W. Willms, and M. Tyree 21

3. Cottonwood seedling recruitment along the Oldman River following the flood of 1995;
by: A.R. Kalischuk, J.M. Mahoney, and S.B. Rood 49

Summary:

In accordance with Agreement #97-0126 between Alberta Environment Protection and the University of Lethbridge, studies were conducted that relate to: (i) monitoring and mitigation of impacts of the Oldman River Dam and (ii) assessments of environmental impacts following the 'Flood of 1995' which produced the highest flows of record throughout southern Alberta.

The present report describes studies relating to the ecology and physiology of riparian (river valley flood plain) cottonwoods (poplars) and impacts of instream flows and disturbance (flood) flows. Progress is described on three study areas:

1. The phenology (timing of development) of riparian cottonwoods is described for the three species present at Lethbridge, the prairie cottonwood, *Populus deltoides*, the narrowleaf cottonwood, *P. angustifolia*, and the balsam poplar, *P. balsamifera*, or almost indistinguishable black cottonwood, *P. balsamifera* subsp. *trichocarpa* (also considered as *P. trichocarpa*). This was used to assess the occurrence of clones, clusters of trees that share a common genotype (genetic make-up) and primarily originated from suckering, the production of new shoots from common roots or buried shoots. The timing of catkin - and bud-flushing, the emergence of reproductive catkins (flower clusters) and subsequently, leaves, was most uniform in members of clones and was reliable for all three species and their native interspecific hybrids.

Using the sex (male or female), species designation and phenological characteristics, a mature cottonwood population at Lethbridge was evaluated for clonal occurrence. 88% of the tree trunks were members of clones, with this proportion being much greater than expected based on the presently incomplete scientific literature. This indicates that clonal replenishment provides a major contribution to cottonwood reproduction in southern Alberta. This is fortunate with respect to conservation and restoration since clonal recruitment can supplement seedling recruitment, which is often negatively impacted by river damming and flow diversion.

2. Correlation analyses of annual branch growth increments, yearly growth segments that are readily visible on cottonwood stems, was conducted with respect to historical stream flow and meteorological patterns. Branch growth was closely correlated with stream flow indicating that (a) cottonwood growth is limited by water availability, and (b) in prairie regions of southern Alberta, the source of water for cottonwoods is the adjacent stream which recharges the riparian water table. The combination of spring stream flow and evaporative water demand which is determined by temperature, sunshine and wind, almost entirely accounted for the historical branch growth pattern. This confirms that physical environmental factors determine cottonwood growth and this relationship will assist in the development of instream flow needs (IFN) analyses for southern Alberta and elsewhere.

3. Following the exceptional flood of early June, 1995, permanent research transects were established along southern Alberta rivers. These permitted the systematic study of cottonwood recruitment following the major flood. A massive seedling recruitment event followed the flood with seedling densities averaging about 400 m^2 at suitable elevations above the stream stage. Seeding die-off continued through 1995 and 1996 and after two years in the order of 95% of the seedlings had died. Even after this mortality, abundant seedlings remain and these are typically reaching about 40 cm in height after two years. Thus, the 1995 flood will probably leave a lasting legacy of cottonwood seedlings that will reinvigorate declining populations along many southern Alberta streams.

The transect studies also demonstrated that clonal replenishment of cottonwood was also promoted by the 1995 flood. New and vigorous saplings emerged as root suckers and from flood training, new shoots from saplings or poles (small trees) that are toppled by the flood flows and buried by deposited sediment. New saplings were also observed to originate from rooted stem fragments but not from abscised branches (in contrast to a literature report). The clonal saplings are faster-growing than seedlings with heights of 1 to 2 m being common after the second growing season. This demonstrates that a flood disturbance promotes clonal as well as seedling recruitment and this will also foster restoration of declining cottonwood stands in southern Alberta.

1.

Characterizing the clonal composition of a cottonwood grove in southern Alberta according to morphology and phenology; by L.A. Gom and S.B. Rood

Abstract:

In the northwestern prairies, the cottonwoods *Populus deltoides* Bartr., *P. balsamifera* L., *P. angustifolia* James, and interspecific hybrids, form the foundation of the riparian forest ecosystem. The present project characterized the phenotype and phenology of each tree in a mature cottonwood grove (N=391) for the purposes of clone-delineation. In order of their utility, the characteristics utilized were tree sex, general leaf-shape, and phenology of flowering, leaf-flushing, senescence, and leaf-abscission. The population's 391 trunks represented only 115 individuals, 67 of which were clones which ranged from 2 to 58 trunks each. Thus, 88% of all trunks belonged to clones, and this high clonal content likely reflects the senior age of the population. Clone structure explained the population's spatial-clumping, female-skewed sex ratio, differential spatial distributions of the sexes and species, and complexity in trunk-size classes. Trends suggest that *P. balsamifera* and *P. angustifolia* are more strongly clonal than *P. deltoides*, partially explaining their differences in environmental preferences. The observed extent of asexual regeneration has implications for riparian resource management and analyses of cottonwood reproductive ecology.

Introduction:

The landscape of south-central and southeastern Alberta is predominated by open treeless prairie. Occasionally these dry expanses are broken by river valleys whose seasonally fluctuating stream flows are capable of supporting native riparian woodlands composed of three cottonwood species, *Populus deltoides* Bartr., *P. balsamifera* L., and *P. angustifolia* James, and the complex of hybrids facilitated by their overlapping ranges (Moss 1944, Brayshaw 1965). Constituting the only native forests in these regions, cottonwoods are essential to a particularly diverse assemblage of other flora and fauna (Bradley et al. 1991).

Cottonwood forests are in decline due to clearing for agricultural and domestic purposes, poor cattle grazing practices, and the regulation of river flows among other factors (Rood and Mahoney 1991). Since cottonwoods form the foundation for the whole riparian ecosystem, their decline signals that the entire system is in danger (World Wildlife Fund Canada and Forestry, Lands and Wildlife, Fish and Wildlife Division 1992). Conservation and management efforts have been impaired by the inadequate understanding of cottonwood regenerative strategies. Efforts have mainly focused on sexual (seedling-based) replenishment, while asexual (clonal) contributions have been largely overlooked. To fully understand the functioning of riparian cottonwood regeneration, the contributions of sexual versus asexual replenishment must be recognized.

Clonal regeneration in cottonwoods can occur via root-suckering, the production of new shoots from existing roots, and shoot-suckering, the production of new shoots from existing, buried shoots. Given the proper conditions, branch fragments can also root, contributing in a less recognized way to asexual recruitment. In the few studies devoted to investigating cottonwood clonal processes, substantial natural shoot-suckering has been documented for *P. deltoides* (Barnes 1985, Bradley 1982, and Rood et al. 1994), *P. balsamifera* (Zasada et al. 1981 and Rood et al. 1994), and *P. angustifolia* (Rood et al. 1994). Natural occurrences of root-suckering have been recorded in *P. balsamifera* (Zasada et al. 1981 and Rood et al. 1994) and *P. angustifolia* (Rood et al. 1994), but not in *P. deltoides* (Bradley 1982 and Rood et al. 1994). However, there is evidence of natural root-suckering in *P. fremontii* (Howe and Knopf 1991 and Irvine and West 1979), which is closely related to *P. deltoides* (both of these species belong to the *Populus* section Aigeiros). Natural rooting of branch fragments is favored in wet climates and has been reported in the section Tacamahaca species, *P. balsamifera* (Zasada et al. 1981) and *P. trichocarpa* (Galloway and Worall 1979), it has also been observed in southern Alberta, although infrequently (Bradley 1982 and Rood et al. 1994).

Rood et al. (1994) systematically excavated 690 cottonwood saplings on the floodplains of four rivers in the Oldman River Basin to determine the relative proportions of sexual versus asexual contributions to recruitment. They concluded that 48% of the saplings originated through clonal mechanisms. However, because recruitment of seedlings is known

to vary between years, this proportion of clonally originated saplings might not be reflected in the mature cohort. Thus, further investigation is needed to appraise the extent of clonal origin among mature trees.

Distinguishing clonally versus sexually originated mature trees is problematic. In isolation, there are no defining characteristics that label a mature cottonwood as a seedling or a clone. The only way to distinguish such origin is to trace clonal relationships between individuals. In the absence of clonal evidence, seedling origin is assumed.

Since members of a genet share a genotype, they also share heritable phenotypic characteristics of morphology and phenology. The usefulness of such characters in clone delineation depends on their environmental insensitivity and degree of variability. Ideal characters will distinguish between but not within individuals. Although not able to prove exact genome matches, detecting differences in genetically conserved traits facilitates the exclusion of dissimilar members from proposed genets, and so serves to narrow the field of putative clones. Accuracy of this delineative method depends on the stringency of the determination of dissimilarity as dictated by the quality of characteristics available.

Clone delineations in aspen species have often involved the use of morphology and phenology in a spatial context (Andrejak and Barnes 1969, Barnes 1959, Barnes 1969, Blake 1964, and Kemperman 1977). Modeled after their approaches, this study likewise investigated cottonwood clonality by analyzing the spatial aggregation of similarly characterized trees.

Methods and Materials:

The approximately 200 X 200 meter study site consists of an artificial island on the Oldman River floodplain. It is defined by a diversion canal excavated in 1956 and is located adjacent to the University of Lethbridge campus in Lethbridge, Alberta, Canada (49°41'N, 112°52'W). Every cottonwood with a trunk circumference at breast height (CBH) of at least 10 cm was numbered with an aluminum tag (N=391). Each tree's position was mapped spatially and an X - Y coordinate assigned.

In 1995 and 1996, every tree was characterized according to sex, leaf shape (species estimate), gall abundance, trunk architecture, and the timing of flowering, leaf-flushing, leaf-senescence, and leaf-drop. Additionally, observations of general health and miscellaneous environmental effects were made throughout the observation periods.

Sex (male or female) was determined for every tree flowering in 1995 by observing its floral characteristics through binoculars. These decisions were verified in subsequent surveys.

A set of six mature leaves, collected from first and second node positions, was photocopied for every tree. Eight leaves were selected from the population to characterize the range of leaf-shape variation present (Fig. 1). These were coded from 1 to 8, with 1 representing pure *P. angustifolia*, 4 being pure *P. balsamifera*, and 8 as pure *P. deltoides*. In this way, codes 1 to 4 encompass the two section Tacamahaca species and their intrasectional hybrids, codes 7 to 8 represent the one Aigeiros species, and codes 5 to 6.5 correspond to the range of intersectional hybrids. Each set of six leaves was classified according to the selected leaf shapes, or given an intermediate code when the shape was transitional.

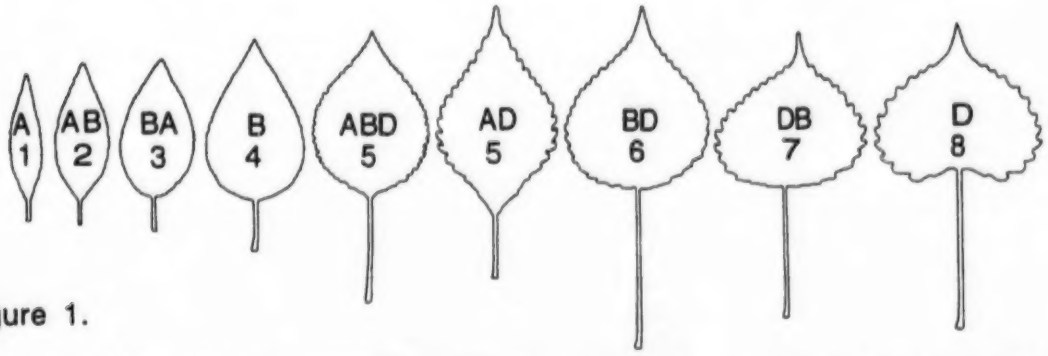


Figure 1.

The eight leaf shapes selected from the population. Letter codes indicate estimated species composition; A = pure Populus angustifolia, B = pure P. balsamifera, D = pure P. deltoides. Mixed letter combinations indicate hybrids, with the first letter indicating the predominant species, except for ABD and AD which represent complex hybrids without a predominant species. Number code equivalents are included to simplify record keeping and analysis.

In conjunction with Kalischuk et al. (1997), *Aceria parapopuli* Keifer galls were surveyed on February 9 and 16, 1996. Gall abundance per tree was estimated by the number of galls counted during a one minute interval through binoculars. The count reached its saturation point at approximately 130 galls per minute.

Trunk architecture was designated 'straight' if there was a single, upright leader-branch, from which smaller branches originated, and the entire form displayed a strong vertical tendency, 'gnarled' if such a leader-branch was absent and the branches tended to spread as far horizontally as vertically, or 'twisted' when there was at least one, fairly vertical, main leader-branch but the other branches tended to spread horizontally as well as vertically.

Complete surveys of phenology were conducted in the spring of 1995 on May 2, 5, 8, 10, 13, 17, 19, 23, 25, and June 1, and in the autumn of 1995 on September 13, 20, 27, October 4, 11, and 19. Stages for each type of phenology were coded as they were distinguishable through binoculars. Male and female flowering phenology was coded 0 through 4 (Fig. 2). Flushing was coded 0.5, 1, and 2, for initial leaf-bud break, leaf emergence, and leaf expansion respectively. Leaf senescence was coded 0 through 9 where the estimated ratio of yellowed foliage was 0, 5, 10, 15, 20, 25, 50, 75, 99, or 100% respectively. Leaf drop was coded 0 through 7 where the estimated ratio of leaves dropped was 0, 5, 10, 25, 50, 75, 99, or 100% respectively. The occurrence of branch sacrifice was recorded as 1, 2, or 3 depending on the number of branches affected.

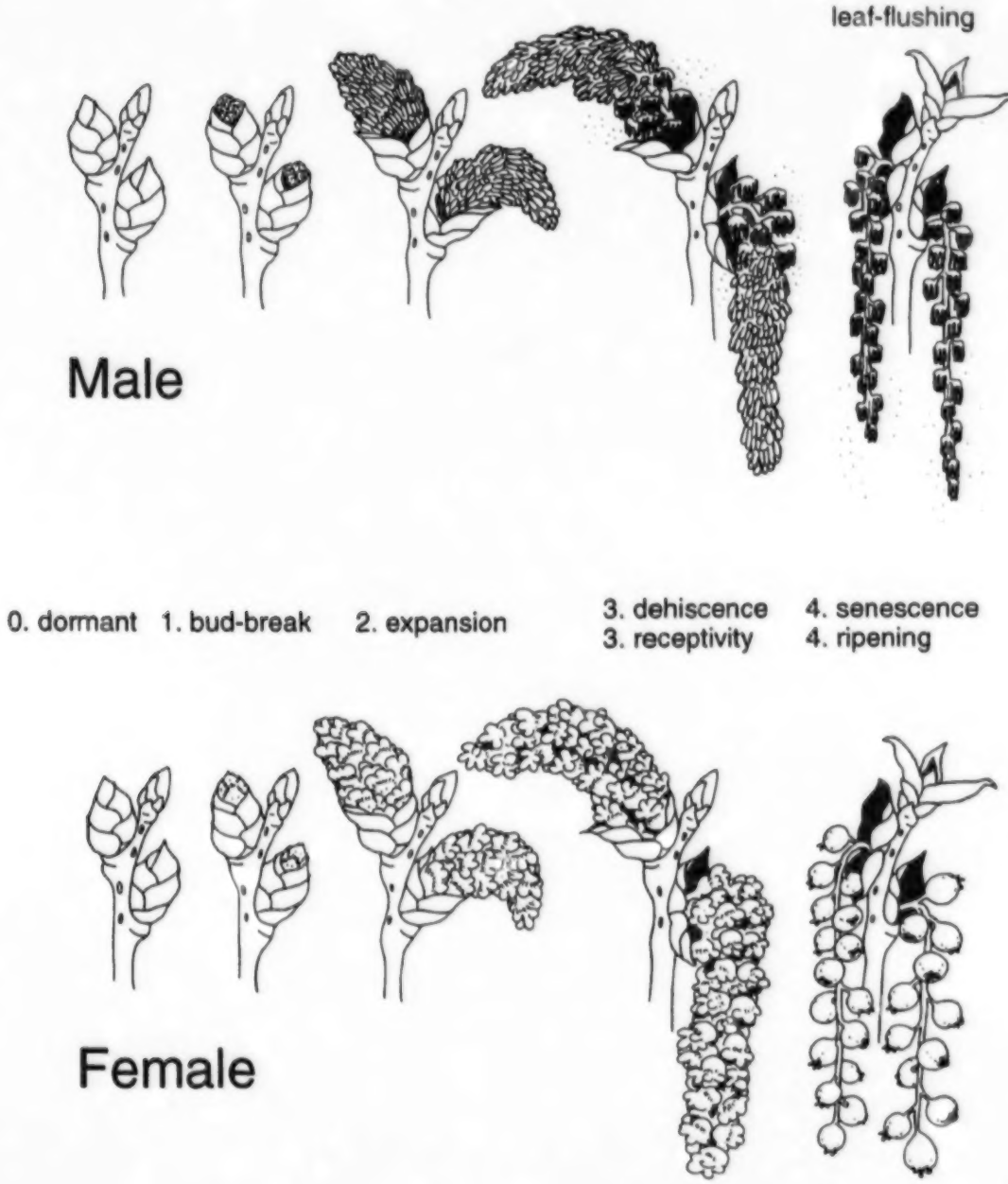


Figure 2. The five flowering stages in male and female cottonwoods

Results and Discussion:

This population's clustered spatial arrangement of trunks was found to coincide with a clumped distribution of sex and species-related characteristics. Patterns in the phenology of flowering, leaf flushing, leaf senescence, and leaf drop were suspected to be species related, with some potential for individual variation. By consolidating the spatial and phenotypic clusters, a map of putative clones was produced.

-Clone delineation-

Division according to sex resulted in two groups; one of 187 trees (116 males + 71 of unknown sex) and another of 275 trees (204 females + 71 of unknown sex). These groups were subdivided according to the leaf shape categories. Overlap was introduced between adjacent shape categories, so that intermediates were considered in either group (Table 1). The resultant twelve groups were then subdivided according to their phenology matrices. The timing of flowering was weighted most heavily, followed by flushing, senescence and abscission. A division was made where differences between codes on any given day exceeded a value of 1. Suspicious jumps in a tree's codes were treated with caution. If missing values were suspected, these differences were not used to guide subdivisions.

Table 1.

The 12 groups created after division by sex and leaf-shape categories.

Females + unknowns		Males + unknowns	
Leaf-shapes	# of trunks	Leaf-shapes	# of trunks
1.0-1.5	16	1.0-1.5	15
1.5-2.5	61	1.5-2.5	47
2.5-3.5	94	2.5-3.5	53
3.5-4.0	59	5.0-5.5	71
5.0-5.5	92	5.5-6.5	23
7.0-8.0	29	6.5-8.0	24

note: overlaps were introduced where sex was unknown or leaf-shape was intermediate

Redundant appearances of trees in more than one clone group were compared. The version most closely matching the group to which it had been assigned was retained. In this way, preference was given to any copy assigned to a group rather than occurring singly.

A final decision on clonal membership was made based on the spatial distances separating the members of each group. If the minimum separation was greater than approximately 20 m, a division was made. As a result, the population of 391 trunks was divided into 67 putative clones (with multiple trunks) and 48 single-trunked individuals (Fig. 3). Mite-gall abundances verified the clonal-identity of the most susceptible of these groups. The characteristics of each clone group are summarized in Table 2.

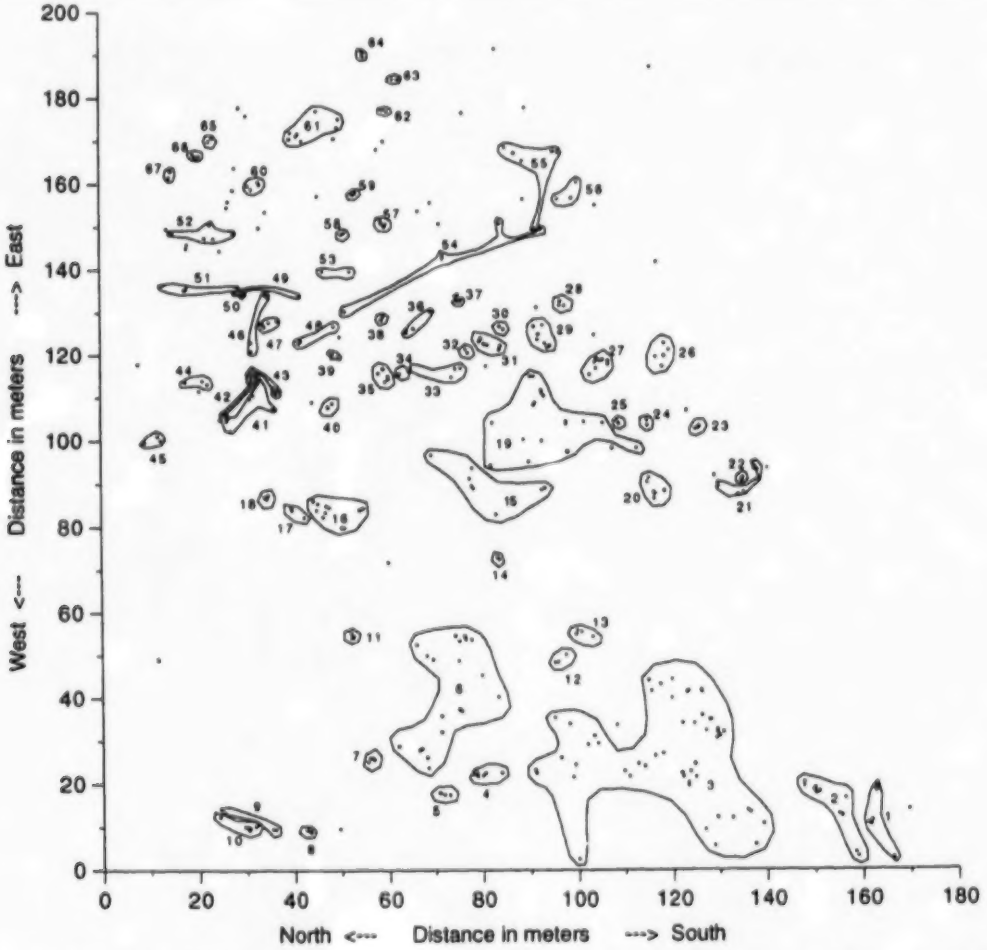


Figure 3. Map of single trunks and hypothesized clone groups (numbered).

Table 2.

Summary of the number of ramets, sex, and species type of each putative clone as indexed by the clone identification numbers.

Clone ID#:	# of ramets:	Clone Sex:	Ave. Species-Type Code	Clone ID#:	# of ramets:	Clone Sex:	Ave. Species-Type Code
1	6	M	2.5	34	2	F	8.0
2	11	F	3.0	35	5	M	5.0
3	53	F	3.5	36	4	M	5.0
4	6	M	3.0	37	2	M	5.0
5	3	F	5.0	38	2	F	7.5
6	20	F	2.5	39	2	F	8.0
7	4	F	2.0	40	2	M	8.0
8	3	F	1.0	41	9	M	3.0
9	3	M	2.0	42	2	M	2.0
10	7	F	1.5	43	5	F	2.0
11	3	F	2.5	44	3	M	2.0
12	3	M	8.0	45	3	F	3.5
13	4	F	4.0	46	4	M	5.0
14	2	F	3.0	47	4	?	5.0
15	8	F	2.0	48	3	M	8.0
16	11	M	1.5	49	3	M	8.0
17	3	F	2.5	50	2	F	5.0
18	3	F	3.0	51	4	F	7.0
19	18	F	5.0	52	5	F	5.0
20	6	M	6.0	53	2	M	2.0
21	5	M	2.0	54	5	F	8.0
22	2	F	8.0	55	6	F	5.0
23	3	F	8.0	56	3	?	5.0
24	2	M	2.0	57	4	M	5.5
25	2	F	5.0	58	2	M	3.5
26	5	M	2.5	59	2	M	5.5
27	8	F	5.0	60	4	F	5.0
28	3	M	5.5	61	8	F	5.0
29	7	F	5.0	62	2	?	3.0
30	2	F	8.0	63	2	?	3.0
31	6	F	5.0	64	2	F	5.0
32	2	F	8.0	65	2	M	5.0
33	4	M	2.5	66	3	M	5.0
				67	2	?	5.0

By focusing on the clustered spatial distribution of phenotypic characteristics in this population, it has been possible to delineate putative cottonwood clones. The characteristics found to be the most effective in tracing these patterns, listed in order of utility, were; sex, leaf-shape (species estimate), phenology, spatial distribution, and gall abundance. Based on the heritability of the traits and the population's spatial clustering, the identification of clonally related individuals has been confident.

-Clonal trends-

Of the clonal trends depicted in Table 3, the only significant difference among the sexes and species-types was that the ratio of clonal to single trunks was significantly higher for females and members of section Tacamahaca (Table 4). The three large, female, Tacamahaca clones; 2, 3, and 6, are at least partially responsible, since the same significance is not seen in comparisons of clonal and non-clonal genets (Table 4).

The number of trunks per genet, and the number of ramets, their spacing, and their range in trunk circumferences within clones did not differ significantly among the sexes or between the three species categories (Table 4). However, the distances of female trunks and mean distances of female genets to the river were significantly shorter than those of males (Table 4). Additionally, section Tacamahaca trunks and genets were significantly closer to the river channel than the intersectional hybrids or members of section Aigeiros (Table 4). The mechanism of this distribution is unclear, but other authors have observed similar spatial segregations of the sexes in cottonwood (Comtois et al. 1986, Ellis 1996), aspen (Il'in 1973, Grant and Mitton 1979), and willow (Crawford 1983, Elmqvist et al. 1988, Dawson and Bliss 1989) species.

To summarize, the average number of ramets per clone was 5.12, the proportion of multiple-trunked genets was 58.26%, the average spacing between ramets was 4.07 m, the average clone diameter was 7.54 m., and the average range in CBH per clone was 0.67 m.. The three large female clones belonging to section Tacamahaca suggest that cottonwoods of this type produce larger numbers of ramets. However, larger numbers of genets need to be surveyed for substantiation.

Table 3.

Summary of numbers of clones and ramets, and inter- and intra-clone distances according to sex and species-categories.

								Inter-Ramet Dist's:		
	C	R	S	(R+S) N	(C+S) G	N/G	R/C	Ave.	Min.	Max.
Whole Site:	67	343	48	391	115	3.40	5.12	4.07	1.06	7.54
Females:	35	224	14	238	49	4.86	6.40	4.51	0.80	9.31
Males:	27	106	24	130	51	2.55	3.93	3.89	1.34	6.19
Unknowns:	5	13	10	23	15	1.53	2.60	1.90	1.44	2.44
Section Tacamahaca	29	193	18	211	47	4.49	6.66	4.79	1.23	9.21
Females:	14	129	9	138	23	6.00	9.21	5.18	0.62	11.37
Males:	13	60	4	64	17	3.76	4.62	4.95	1.91	8.15
Unknowns:	2	4	5	9	7	1.29	2.00	0.99	0.99	0.99
Intersectional Hybrids	25	115	19	134	44	3.05	4.60	3.16	0.92	5.72
Females:	12	71	1	72	13	5.54	5.92	4.03	0.86	8.10
Males:	10	35	13	48	23	2.09	3.50	2.30	0.74	3.56
Unknowns:	3	9	5	14	8	1.75	3.00	2.51	1.75	3.41
Section Aigeiros:	13	35	11	46	24	1.92	2.69	4.21	0.98	7.32
Females:	9	24	4	28	13	2.15	2.67	4.13	0.99	7.71
Males:	4	11	7	18	11	1.64	2.75	4.40	0.96	6.43
Unknowns:	0	0	0	0	0	N/A	N/A	N/A	N/A	N/A

C= # of clonal genets
R= # of ramets (clonal trunks)
N= # of all trunks
G= # of all genets
S= # of single / non-clonal trunks

Table 4.

Tests for sex and species related differences in clonality.

	Males vs. Females:			Species Categories:		
	Chi square			Chi square		
	X^2	df	P	X^2	df	P
# of single, vs. clonal trunks (S vs. R)	14.3673	1	< 0.0001 *	8.9833	2	0.0119 *
# of multiple, vs. single-trunk genets	3.6253	1	0.0595	0.4320	2	0.8248
	t-tests			Analyses of variance		
	t	df	P	F	df	P
# of trunks per genet (N/G)	1.9386	55	0.0577	1.8558	114	0.1611
# of ramets per clone (R/C)	1.3770	60	0.1736	1.6563	66	0.1989
ave. distance between ramets	0.5259	60	0.6009	0.8908	66	0.4154
min. distance between ramets	1.4528	28	2.0484	0.4168	66	0.6609
max. distance between ramets	1.1625	60	0.2496	0.7832	66	0.4613
range in CBH for clones	0.6579	60	0.5131	1.9820	66	0.1462
trunk distance to river	5.3023	318	< 0.0001 *	138.7345	390	< 0.0001 *
mean genet distance to river	2.1822	98	0.0315 *	13.700	114	< 0.0001 *

note: the species categories were section Tacamahaca, intersectional hybrids, and section Aigeiros

-Clonal implications-

This study has revealed evidence of extensive clonality in cottonwoods. Approximately 88% of trunks had clonal relaticnships, and 58% of genetic individuals were clones (had multiple trunks). Considering that such a large proportion of the population is directly influenced by clonality, there are widespread implications to cottonwood population biology.

Clonal versus seedling reproduction differ adaptively (Table 5) such that cottonwoods could benefit by the complimentary use of both sexual and asexual regenerative strategies. Seedling-based reproduction facilitates recruitment in the high-disturbance environments of meandering river floodplains (Bradley and Smith 1986), while clone-based strategies can exploit the highly competitive environments within stands. As expected, seedlings dominate young floodplains, and asexual sprouts appear as groves age. Since clones expand over time, older forests like this one show strong evidence of clonality.

Table 5.

The advantages and disadvantages of sexual (seedling) versus asexual (clonal) strategies in cottonwood reproduction/regeneration.

	Reproductive Unit:	
	Seedling	Clone
dispersion ability	(+) high	(-) low
genetic variability	(+) high	(-) low
parental investment (per individual)	(+) low	(-) high
survival rate (per individual)	(-) low	(+) high
maturation rate	(-) long	(+) short
competitive ability	(-) low	(+) high

note: (-) identifies a disadvantage, and (+) identifies an advantage.

Cottonwoods are the foundation for the riparian forest ecosystem. Their capacity to regenerate asexually as well as sexually has important applications in riparian resource management. However, the promotory conditions, natural rates of cottonwood asexual regeneration, and implications to genetic diversity are not fully understood. Further investigation into these areas is required.

Clonality is an advantage in environments less conducive to cottonwood seedling regeneration. Lesser clonal ability may have contributed to the range restrictions of cottonwood species like *P. deltoides*. Tacamahaca species (*P. trichocarpa*, *P. balsamifera*, and *P. angustifolia*) survive in environments with steep gradients, coarse beds, and constrained channels, where asexual regeneration maintains forests between the infrequent opportunities for sexual regeneration. Alternatively, *P. deltoides* occurs more frequently on freely meandering or braided channels with low gradients and sandy beds, where sexual regeneration is more frequently successful, and so asexual regeneration is less necessary. It is unclear if the more clonal species are reversely restricted by reduced seedling success.

Since a forest's clonal content increases as it matures, strongly clonal species would be expected to dominate over time. If the southern Alberta species differ in their clonal abilities, the globally unique, tri-specific, hybrid swarm could be jeopardized by the loss of regular seedling establishment opportunities.

Clonal sprouting in mature cottonwood groves influences the physical structure of the forest by complicating its age, size, and spatial distributions. Such forest complexity enriches wildlife habitat (Hunter 1990). High structural diversity translates into more foraging and sheltering opportunities, which are especially important in accommodating greater numbers and diversities of birds (Saunders and Cordes 1989).

Since ramets represent genome duplications, those genotypic proportions can become amplified, causing skew in the population. When each trunk was considered separately, the strongly female-biased sex ratio (204:116 ; X^2=24.20, df=1, P< 0.0001), was not significantly different from 2:1 (X^2=1.22, df=1, P=.3641). However, this skew is now explained by the disproportionately high number of female ramets. The sex ratio of genets

(49:51) was found to be unbiased towards either sex (X^2=0.04, df=1, P=0.8814). Even when genets of unknown sex were counted as males, the sex ratio (49:66) was not significantly skewed (X^2=2.513, df=1, P=0.1349).

Clonal effects can be misinterpreted in population studies where clonal structure is not recognized. In addition to the skewing of characteristics, shifts in the spatial distributions of sex and species over time can be forms of clonal artifact. For example, although physiological differences between the sexes might have contributed to instances of their spatial segregation in cottonwood (Comtois et al. 1986, Ellis 1996), aspen (Il'in 1973, Grant and Mitton 1979), and willow (Crawford 1983, Elmqvist et al. 1988, Dawson and Bliss 1989) species, it is important to recognize that such distributions may have been greatly exaggerated by clonal effects.

In summary, the patterns of phenotype and phenology revealed in this study are best explained by a history of extensive cottonwood clonality. It is strongly recommended that this asexual potential be investigated for other populations to achieve better understanding of cottonwood reproductive ecology and population dynamics.

References:

Andrejak, G.E. and B.V. Barnes 1969. A seedling population of Aspens in southeastern Michigan. Mich. Bot. 8: 189-202.

Barnes, B.V. 1959. Natural variation and clonal development of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan. Ph.D. Thesis, University of Michigan, Ann Arbor.

Barnes, B.V. 1969. Natural Variation and Delineation of Clones of *Populus tremuloides* and *P. grandidentata* in Northern Lower Michigan. Silvae Genet. 18: 130-142.

Barnes, W. 1985. Population Dynamics of Woody Plants on a River Island. Can. J. Bot. 63: 647-655.

Blake, G.M. 1964. Clone identification and delineation in the aspens. Ph.D. Thesis, Univ. of Minnesota, Minneapolis.

Bradley, C.E. 1982. Modified Meandering River Regimes - Effects on Plains Cottonwood Regeneration. M.Sc. Thesis, Univ. of Calgary, Alberta.

Bradley, C.E., F. Reintjes, and J.M. Mahoney 1991. The biology and status of riparian poplars in southern Alberta. World Wildlife Fund Canada and Forestry, Lands & Wildlife, Fish & Wildlife Division.

Bradley, C. and D. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Can. J. Bot. 64: 1433-1442.

Brayshaw, T.C. 1965. Native poplars of southern Alberta and their hybrids. Can. Dept. For. Pub. No. F047-1109.

Comtois, P., J.P. Simon, and S. Payette. 1986. Clonal constitution and sex ratio in northern populations of balsam poplar *Populus balsamifera*. Holarctic Ecol. 9: 251-260.

Crawford, R.M. and J. Balfour. 1983. Female predominant sex ratios and physiological differentiation in arctic willows. J. Ecol. 71: 149-160.

Dawson, T.E. and L.C. Bliss. 1989. Patterns of water use and the tissue water relations in the dioecious shrub, *Salix arctica*: the physiological basis for habitat partitioning between the sexes. Oecologia 79: 332-343.

Ellis, L.M., M.C. Molles, and C.S. Crawford. 1996. Seasonal flooding and riparian forest restoration in the Middle Rio Grande valley. Prepared for: U.S. Fish and Wildlife Service, Albuquerque, New Mexico. Cooperative Agreement 14-16-0002-91-228. 212 p.

Elmqvist, T., L. Ericson, K. Danell, and A. Salomonson. 1988. Latitudinal sex ratio variation in willows, *Salix* spp., and gradients in vole herbivory. Oikos 51: 259-266.

Galloway, G., and J. Worrall 1979. Cladoptosis: a reproductive strategy in black cottonwoods? Can. J. For. Res. 9: 122-125.

Grant, M.C. and J.B. Mitton. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evol. 33: 914-918.

Howe, W.H., and F.L. Knopf 1991. On the Imminent Decline of Rio Grande Cottonwoods in Central New Mexico. Southw. Nat. 36: 218-224.

Hunter, M.L. 1990. Wildlife, Forests, and Forestry: Principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, NJ. 370 p.

Il'in, A.M. 1973. Sex Ratio in the Aspen under different conditions of growth. Ekologiia 2: 162-163.

Irvine, J.R., and N.E. West 1979. Riparian Tree Species Distribution and Succession along the Lower Escalante River, Utah. Southwestern Naturalist 24: 331-346.

Kalischuk, A.R., L.A. Gom, K.D. Floate, and S.B. Rood 1997. Intersectional cottonwood hybrids are particularly susceptible to the poplar bud gall mite. Can. J. Bot. (in press).

Kemperman, J.A. 1977. Aspen clones: development, variability, and identification. Minist. Nat. Resour. Ont. For. Res. Inf. Pap. No. 101. NTIS, Minist. Nat. Resour. Ont. For. Res. Inf. Pap. No. 101.

Moss, E.H. 1944. The prairie and associated vegetation of southwestern Alberta. Can. J. Res. Sect. C, 22: 11-31.

Rood, S.B., C. Hillman, T. Sanche, and J.M. Mahoney. 1994. Clonal reproduction of riparian cottonwoods in southern Alberta. Can. J. Bot. 72: 1766-1774.

Rood, S.B. and J.M. Mahoney. 1991. The biology of riparian cottonwood forests in the Oldman River Basin. Oldman River Dam Mitigation Program Downstream Vegetation Project Report - Volume I. Prepared for Alberta Public Works, Supply and Services. 155 p.

Saunders, E.J. and L.D. Cordes. 1989. Avian ecology of major habitat types in Dinosaur Provincial Park, Alberta. Prepared for: Alberta Recreation, Parks and Wildlife Foundation. 81 p.

World Wildlife Fund Canada and Forestry, Lands and Wildlife, Fish and Wildlife Division. 1992. Conservation and management strategy for riparian forests in southern Alberta. 36 p. ISBN: 0-86499-903-8.

Zasada, J.C., L.A. Viereck, M.J. Foote, R.H. Parkenson, J.O. Wolff, and L.A. Lankford, Jr. 1981. Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. For. Chron. 57: 57-65.

2.

Branch growth of riparian cottonwoods: A hydrologically sensitive dendrochronological tool.

by J. Willms, S.B. Rood, W. Willms, and M. Tyree

Abstract:

The conservation of riparian (river valley flood plain) forests relies on the provision of instream flows that are sufficient to sustain tree growth. In the present study, annual branch growth increments were investigated as an indicator of environmental favorability for growth of riparian cottonwoods. Trees of three species, *Populus angustifolia*, *P. balsamifera*, and *P. deltoides*, and their natural interspecific hybrids, were studied at five sites along the Oldman and South Saskatchewan rivers in Alberta, Canada. Annual branch growth increments for the interval from 1983 to 1992 were closely positively correlated with stream flows (r^2=0.79 at Lethbridge) and slightly negatively correlated with weather variables that contribute to water demand: evaporation, temperature, wind, and/or sunshine. The combination of January to May stream flow (water supply) and June evaporation (water demand) almost entirely accounted for the branch growth variation across years (r^2=0.91 at Lethbridge). Tree ring increments were also investigated but were more complacent (less variable) than branch increments and less closely correlated across trees at a site or with stream flow or other environmental variables. Analysis of branch growth increments thus provides an accurate but short duration (one or two decades) record of environmental favorability for growth. The close correlation between branch growth and stream flow indicates that water is the principal limitation to riparian cottonwood growth and that these trees obtain their water from a source linked to the stream, the riparian water table. Analyses of branch increments should provide a management tool for (i) determining instream flow needs for riparian cottonwoods and (ii) analyzing impacts of stream flow alterations due to river damming or water diversion.

Introduction:

Riparian cottonwoods include various *Populus* species that are well adapted to the geomorphologically dynamic zones adjacent to meandering streams. These trees provide the foundations for forest ecosystems that provide environmental, aesthetic and recreational relief in the otherwise

treeless arid and semi-arid areas of western North America. Riparian forests provide the richest wildlife habitats in these regions as they provide forage, cover and other other resources for a wide variety of animals, including abundant birds (Finch and Ruggiero 1993). These woodlands are principally comprised of cottonwoods, with different species overlapping in distribution and hybridizing to further contribute to the biodiversity of the riparian forest ecosystems (Eckenwalder 1984, and Rood et al. 1986).

While riparian cottonwoods are ecologically especially valuable, these trees are also particularly vulnerable. About three-quarters of southwestern American cottonwood forests have been lost in the past two centuries (Johnson and Haight 1984). River valleys are preferred areas for livestock and crop production as well as urban development and transportation corridors. Stream dewatering due to river damming and water diversion for irrigation, urban or other use has also had widespread and sometimes devastating impacts on the cottonwoods (Johnson et al. 1976, Crouch 1979, Bradley and Smith 1986, Fenner et al. 1985, Rood and Heinze-Milne 1988, and Rood and Mahoney 1990).

Negative impacts of artificially reduced river flows would be expected if riparian cottonwoods are dependent on the stream as their water source. This is generally assumed to be the case and consistent with the distribution of cottonwoods that are generally restricted to narrow corridors along river valley flood plains. Oxygen and hydrogen isotopic analyses support this interpretation (Busch et al. 1992) although alternate water sources also occasionally occur (Dawson and Ehlringer 1991).

One method of assessing the water source for tree growth is to investigate correlations between tree growth and water availability from different sources. Precipitation is the principal water source for non-riparian trees and for more than a century, correlations have been reported between precipitation patterns and annual tree ring increments (Glock 1941, and Fritts 1976).

Stream flows vary substantially across years and correlations between tree ring increment and stream flow have also been reported for some riparian trees (Johnson et al. 1976, and Stromberg and Patten 1990). For example, in black cottonwoods (*P. trichocarpa*, a close relative or

subspecies of *P. balsamifera*), correlations were observed between tree ring increments and combinations of same and prior year stream flows (Stromberg and Patten 1991, and 1996). This correlation was further investigated as a method of determining instream flows needs (IFN) of riparian cottonwoods; IFN define the water requirements necessary to support various components of riverine and riparian ecosystems. Stromberg and Patten (1991) concluded that black cottonwoods in the California's Sierra Nevada's required annual radial growth of three to four mm to maintain a healthy tree canopy and that 40 to 60% of the natural stream flow was required to sustain that level of growth.

However, tree rings of riparian cottonwoods can be complacent, demonstrating little variation across years and a lack of systematic influence due to stream flow alteration (Johnson et al. 1976, and Reily and Johnson 1982). This reduces the value of ring-based dendrochronological approaches for determining water source or IFN. Alternative growth measures may be considered and researchers have demonstrated that height growth of various trees also reflects water availability (Hiley 1923, and Herman 1956). However, height growth can only be practically measured on small trees and inherent patterns in height growth during juvenile establishment confound the study of environmental influence.

Annual branch growth increments provide an alternative to either radial increments or height growth but have largely been neglected as a potential method of monitoring environmental influence on tree growth. Darrow (1943) found a positive relationship between branch growth increment and spring and summer precipitation of *Fouquieria splendens* (ocotillo). In surveying the tree growth responses following the North American drought of the 1930's, Albertson and Weaver (1945) concluded that drought decreased growth rates of leaf areas, radial increments and branches. Stromberg and Patten (1989) have partially investigated the use of branch growth increment analysis and reported close correlation (r^2 = 0.67) with same year stream flow for black cottonwoods (*P. trichocarpa*) in the California Sierras. This demonstrated relationship provides promise for an alternate dendrochronological approach for ecophysiological investigation and as a tool for river resource management. Conversely, Randall and Patten (1991) did not find branch growth increments, which they referred to as internodal stem growth, sensitive to differences across stream environments in a study along the Salt River, Arizona.

A number of factors favor the analyses of branch growth increments as quantitative indicators of environmental influence on cottonwood growth. Water condition has a particularly strong impact on branch elongation growth since cell and organ elongation are the physiological processes most responsive to water status (Hsaio 1973). Branch growth may be even more sensitive to water stress than height growth (Hinckley et al. 1991), presumably reflecting the apical dominance that favors the apical region during physiological stress. Branch growth may also be less inhibited by tree crowding than radial growth (Tryon et al. 1957). The occurrence of numerous branches per tree enables statistical subsampling as well as the rejection of individual shoots that have been browsed, diseased or otherwise damaged. In measurement scale, branch growth increments are much larger than radial growth increments, decreasing the proportional error due to measurement inaccuracy. Unlike tree ring analyses, branch growth increments can be simply and quickly measured in the field without the need for core extraction and subsequent microscopic observation. The measurements are nondestructive and repeated measurements of the same branches are possible.

Due to these potential advantages, the present study was conducted: (i) to investigate the usefulness of annual branch growth increments as quantitative indicators of historical environmental condition and particularly, water availability, on tree growth, and (ii) to specifically investigate the possible relationship between stream flow and the growth of riparian cottonwoods in southern Alberta, with this second objective as a means of clarifying the water source for these trees. The satisfaction of these two goals would provide a quantitative method that would contribute to the determination of IFN of riparian cottonwoods. This alternate dendrochronological approach would contribute another method for the analysis of potential impacts of river damming and river flow management on the growth of riparian cottonwoods and correspondingly provide a useful tool for environmental resource evaluation and management.

Methods and materials:

-Study Area-

In 1993 and 1994, branch growth increment measurements and increment cores were taken from three riparian cottonwood species, the narrowleaf cottonwood (*Populus angustifolia*), the balsam poplar (*P. balsamifera,* and/or the virtually indistinguishable black cottonwood, *P. balsamifera* subsp. *trichocarpa* or alternately, *P. trichocarpa* (Brayshaw 1965)) and the prairie cottonwood (*P. deltoides*) and various native interspecific hybrids at five riparian sites in southern Alberta (Figure 1). Fort Macleod trees were located along the north bank of the Oldman River near the inflow of Willow Creek (49°45'N; 113°23W). Trees at Lethbridge were at three sites, one along the east side of the Oldman River at Indian Battle Park (IBP; 49°42'; 113°52'W), the second was along the west bank at the University Grove (UG; 49°41'; 113°51'), south of the Whoop-Up Drive Bridge while the third was along the opposite bank, adjacent to the Coalbanks Canal (CC; 49°41'; 113°51'), an artificial channel excavated as part of the municipal water supply intake system. The municipal intake canal was previously located near and above the CC grove and this probably recharged the riparian water table at that site and would thus have complicated the hydrologic status. Trees at Medicine Hat were along the north bank of the South Saskatchewan River near the western edge of Police Point Park (50°02'N; 110°39'W).

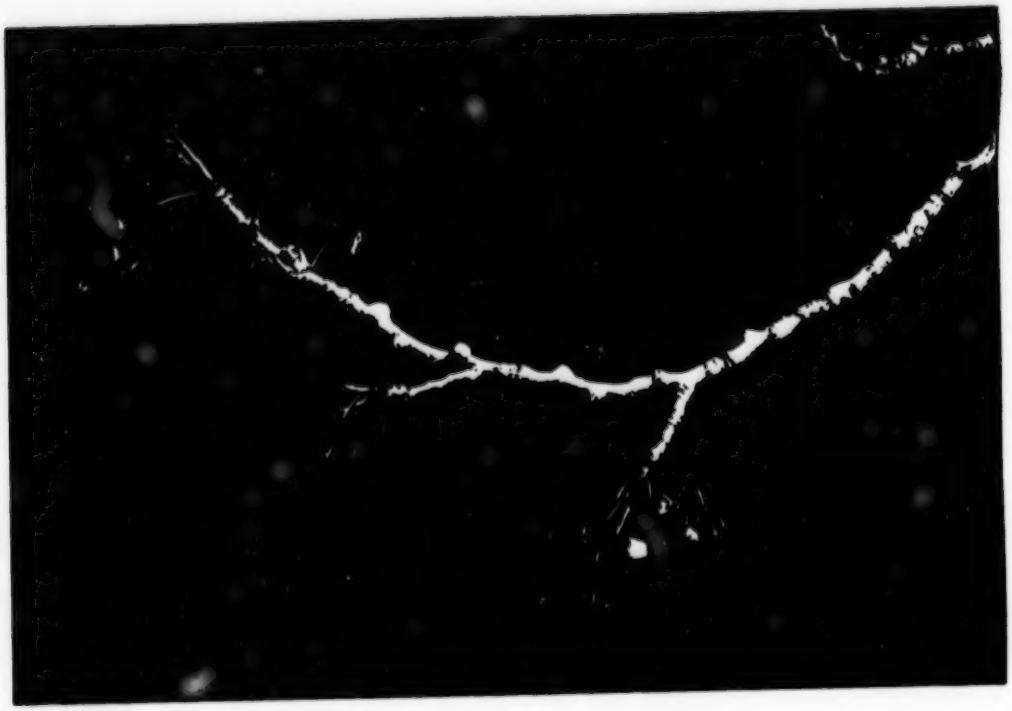


Figure 1.

Photograph of a typical cottonwood branch (*P. deltoides*) showing annual scars that separate annual branch growth increments.

-River Flows-

The Oldman and subsequently, South Saskatchewan rivers originate in the Rocky Mountains of southwestern Alberta and their flow consists primarily of snow melt and rainfall in the Rocky Mountains and foothills. Precipitation in Lethbridge averages 30 cm annually, with much of that falling as snow during the winter months. Due to the frequent chinook winds in the winter and spring, much of the prairie snow-fall sublimes or alternately melts and then either evaporates or infiltrates into the soil. Relatively little prairie run-off contributes to the flow of the Oldman or South Saskatchewan Rivers and thus these are 'exotic' streams, those in which flows reflect distant rather than local precipitation.

The flow of the Oldman River is first (substantially) modified by the Lethbridge Northern Irrigation District (LNID) weir, slightly upstream of Fort Macleod. That weir primarily diverts water offstream during the irrigation season of May through September resulting in downstream flow reductions during that period (Rood and Mahoney 1991). Two major tributaries join the the Oldman River between Fort Macleod and Lethbridge, the St. Mary and Belly Rivers, and both are modified through damming and diversion (Rood and Heinze-Milne 1988, and Rood et al. 1995). Onstream reservoirs are located on both tributary systems and contributions to the Oldman River are reduced throughout the summer months.

More than ten dams exist on the Bow River and its tributaries resulting in annual flow stabilization as well as flow reduction due to diversion for irrigation. The Bow River joins the Oldman River mid-way between Lethbridge and Medicine Hat to form the South Saskatchewan River. Reflecting the combination of alterations to flows to the Oldman and Bow rivers, the flow of the South Saskatchewan is (a) reduced due to irrigation diversion from both the Oldman and Bow Rivers, and (b) flow stabilized due to the flow pattern of the Bow River.

Daily and monthly means of stream flow for 1982 to 1993 were obtained from Environment Canada Surface Water Data and from Alberta Environment Protection Technical Services and Monitoring Division Records Centre. The data had been recorded at the following hydrometric gauging stations: Oldman River near Lethbridge (#05AD007), and South Saskatchewan River at Medicine Hat (#05AJ001). Fort Macleod stream flow

was estimated by subtracting flow diverted by the Lethbridge Northern Irrigation District canal (#05AB019 for 1986-1993; #05AB016 for years prior) from flow at the Oldman river near Brockett (#05AA024).

-Measurements of Cottonwood Branch Increments-

Trees were individually selected based on (i) relatively large size (diameter greater than 60 cm at 1 m height), (ii) position within 50 m of the river, and (iii) the occurrence of several branches that were accessible and had obvious annual growth increments spanning a minimum ten year period. Branches were selected that had no obvious damage such as that caused by browsing or insect infestation. Measurements of individual annual growth increments (Fig. 1) were recorded until the bud scars could no longer be accurately determined or until the branch joined a larger branch. The subsequent analyses focussed on data from the period of 1983 - 1992. At Lethbridge and Fort Macleod sites, three cores were extracted from each tree with an increment borer. Leaves were collected from each tree and leaf measurements were taken to evaluate cottonwood species or hybrid composition. Generally, ten branches were measured for each of ten trees at each site.

Average branch growth per tree was calculated and a weighted values were assigned to each year of measurement using the number of measurements for that year. Average weighted growth per year was subsequently calculated for each site. This weighting compensated for the variation in number of observations per year per tree but ultimately had very little influence on the overall patterns or correlations.

Increment cores were shaved and measured to 0.05 mm under a dissecting microscope at 12 x magnification. Average core increments were calculated from the three values for each year for each tree at each site. No differential weightings were assigned since all cores extended beyond the period of record analyzed in the present study.

-Historical Climatological Data-

Monthly mean meteorological data were calculated from daily data collected between April and September for 1983 to 1993 at the Lethbridge Research Center of Agriculture and Agri-Foods Canada, and from the Atmospheric Environment Service of Environment Canada for weather

stations at Lethbridge and Medicine Hat. The Lethbridge meteorological data were used for Fort Macleod analyses with those data having been collected about 40 km from the Fort Macleod study site.

The meteorological variables that were used in the statistical analyses included monthly mean temperatures and monthly totals of pan-evaporation (mm), total wind (km), precipitation (mm), and sunshine hours. For Medicine Hat, mean wind speed was used rather than total wind distance and total sun hours and pan-evaporation were not available. Mean wind speeds were calculated from wind frequencies by multiplying the mid-point of the speed classes by the number of occurrences and dividing by total number of hours measured.

-Statistical Analyses-

Linear correlation analyses were conducted on the following: average branch growth within trees, average branch and radial growth within sites, average branch and radial growth between sites and with each meteorological and hydrological variable. Maximizing R-Square Improvement regression analyses (SAS) were also conducted with average annual branch and ring increments per site regressed against combinations of the hydrological and meteorological variables.

Results and discussion:

While it has long been recognized that variation exists across branch growth increments, the causes of such variation have not been fully determined (Kozlowski 1964). It was clear from the onset of the present study that annual branch growth increments varied substantially in the riparian cottonwoods, with adjacent increments on healthy branches varying more than four-fold (Figures 2 and 3). Such variation was often consistent across branches within a single tree, indicating that the variation was systematic and associated with the physiological condition of the overall tree (Figure 3).

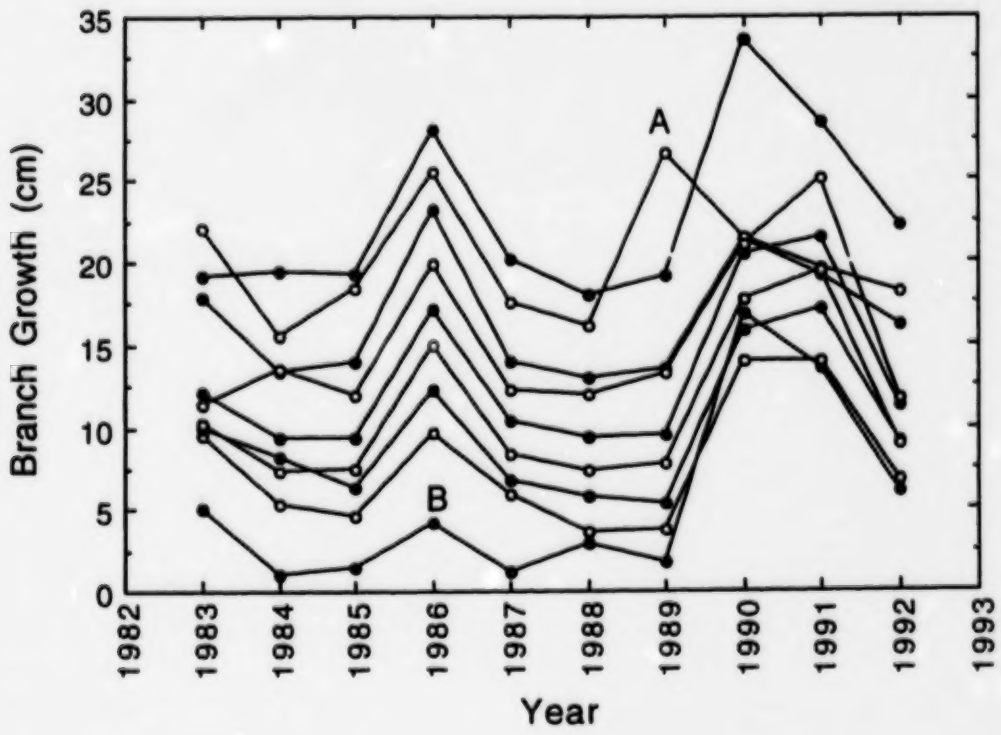


Figure 2.

1983 to 1992 annual branch growth increments of nine branches of one tree (*Populus angustifolia x P. balsamifera*- tree UG3) growing in the University Grove along the Oldman River at Lethbridge, Alberta. For figure clarity, plots are progressively offset upwards by 2 cm and symbols include alternately open and closed circles.

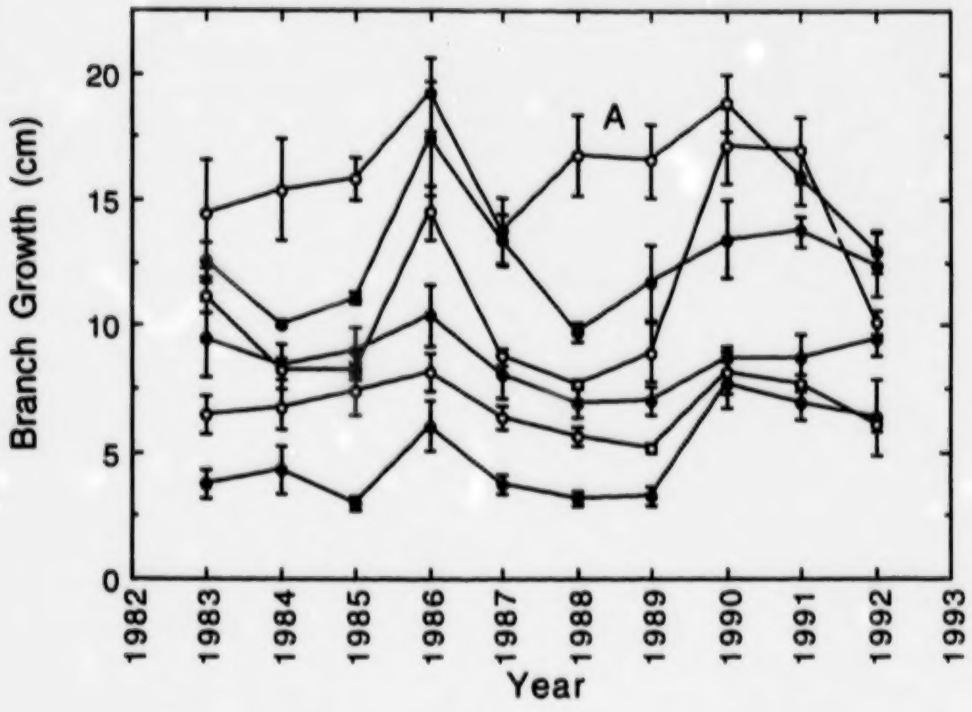


Figure 3.

Mean (± s.e.) branch growth of five riparian cottonwood trees growing in the University Grove along the Oldman River at Lethbridge, Alberta. For figure clarity, plots are progressively offset upwards by 3 cm and symbols include alternately open and closed circles.

However, not all branches demonstrated consistent growth patterns. Obviously damaged branches were excluded from the present study, but even apparently healthy branches demonstrated some differences in growth pattern. Within trees sampled at the five sites, the proportion of branches within individual trees that demonstrated significant ($P<0.05$) correlations in growth pattern ranged from 12 to 47% and averaged 28% (Table 1). In comparing sites, the highest and lowest proportions of trees showing correlations across branches were at Lethbridge along opposite banks of the Oldman River. The Coalbanks Canal (CC) site had the lowest proportion correlated and was the most artificially impacted of the five sites since its grove was influenced by an artificial canal. The data from the CC trees were included in statistical analyses even though this probably reduced the overall extent of correlations and fit (Tables 1 and 2). Consequently, the numerical analyses of the present study are consistently conservative.

Branch growth increment patterns were frequently significantly correlated across trees at specific sites (Figure 4, Table 1). At the different sites, the proportions of correlated trees were generally similar to the proportions of correlations within trees (Table 2). In both cases, the greatest consistency was observed at the University Grove, a relatively natural woodland which has been previously investigated with respect to water relations (Tyree et al. 1994).

The Lethbridge site contains all three cottonwood species and their hybrids, whereas the Fort Macleod site contains only the Tacamahaca section species, the narrowleaf cottonwood, *P. angustifolia*, and the balsam poplar, *P. balsamifera*. The warmer and dryer Medicine Hat site contains only the Aigeiros section species, the prairie cottonwood, *P. deltoides*. Highly significant correlations were observed within trees of all three species and at the Lethbridge site, across individual trees of all three species. Of the Lethbridge trees, 11, 4, and 3 trees had leaf shapes typical of *P. deltoides*, *P. balsamifera*, and *P. angustifolia*, respectively. The greater number of *P. deltoides* reflected its suitability for analysis - large *P. deltoides* trees with numerous branches suitable for measurement were more common than trees of the other species. For each of the three species, most individuals demonstrated reasonable correlation across branches and for each species, at least one tree occurred with little correlation across branches. Thus, all three species are suitable for branch growth analysis but *P. deltoides* is the most useful due to its architecture.

Table 1 .

Proportion of significant ($P<0.05$) correlations in annual growth increments for branches subsampled within individual trees and for average branch growth and average tree ring increment across trees at specific sites along the Oldman and South Saskatchewan rivers, Alberta (n represents number of comparisons).

	Percent correlation in:					
	branch growth per tree		branch growth of trees at a site		tree rings of trees at a site	
Site:	%	(n)	%	(n)	%	(n)
Oldman River						
Lethbridge:						
- Indian Battle Park	16.8	(232)	17.8	(28)	4.7	(21)
- University Grove	46.9	(207)	40	(15)	13.3	(15)
- Coalbanks Canal	12.2	(82)	20	(10)	10	(10)
Total Lethbridge	28.0	(521)	21.6	(171)	7.4*	(136)
Oldman River						
Fort Macleod:	26.7	(136)	26.7	(15)	0	(15)
South Saskatchewan River						
Medicine Hat:	26.7	(446)	34.5	(55)	not analyzed	
Overall	27.6	(1624)	24.8	(294)	7.13	(197)

*In addition to 10 of 136 comparisons of trees from total Lethbridge sites that produced a significant ($P<0.05$) positive correlation, 4 comparisons (2.9%) showed a significant negative correlation across trees.

Table 2.

Correlations (r) between 1983 to 1992 annual branch increments and annual ring increments across sites for riparian cottonwoods of southern Alberta. Significant correlations are in bold with probabilities in brackets.

	LR	FMB	FR	Medicine Hat branches
Lethbridge branches (LB)	**0.616** (0.05)	**0.666** (0.03)	-0.573	0.518
Lethbridge rings (LR)		0.342	-0.301	0.337
Ft. Macleod branches			-0.365	0.310
Ft. Macleod rings (FMR)				0.266

This conclusion that all three species are suitable for the analysis is also supported by comparisons across sites. As indicated, only the Tacamahaca section species *P. angustifolia* and *P. balsamifera* occurred at Fort Macleod while only the Aigeiros section species *P. deltoides* occurred at Medicine Hat. Relatively similar proportions of branches within and across trees showed significant correlations at these two sites (Table 1).

Having confirmed that there was partially consistent variation within trees and within sites, the study subsequently investigated the environmental conditions with which the branch growth variation was most closely correlated. We and others have repeatedly determined that water status is often limiting for riparian cottonwoods in this region and in other semi-arid regions and further determined that stream flows underlie some of the availability of water for riparian cottonwoods in this region (Bradley and Smith 1986, Rood and Heinze-Milne 1988, and Rood et al. 1995). Consequently, it was hypothesized that patterns of branch growth variation would reflect historical stream flows. The other potential source of water, local precipitation, was also investigated, along with weather characteristics that would relate to both water demand and growth capacity: wind, temperature and sunshine.

The annual branch increments represented the total growth over a single season and would thus integrate the growth that occurred on all individual days or weeks. Annual branch growth increments provide an integrated record of growth over each year, in contrast to water potential, diffusive resistance or abscisic acid measurements that reflect more immediate physiological responses. The integrative nature of branch growth analyses makes these especially valuable for broad time-scale river resource management studies. However, more instantaneous physiological measures would also complement branch growth increment analyses in revealing specific short-term management impacts, such as diurnal stream patterns associated with hydroelectric generation or the specific impacts of insufficient stream flows during specific days or weeks or impacts due to abrupt flow changes or short-term extreme flow reductions.

Due to the integrative nature of the annual branch increments, it was considered appropriate to conduct the correlation analysis on monthly hydrologic and climatic data. Even yearly data were sufficient to reveal the principal correlations and it is therefore unlikely that substantial improvement of correlation fit would result from analyses involving a shorter duration weekly or daily time step for the environmental data.

Correlation analyses with individual environmental variables confirmed the principal hypothesis that branch growth was particularly correlated with stream flow. When considering only monthly variables, May (r^2=0.74) and March (r^2=0.65) stream flow best described branch growth of Lethbridge trees. Subsequent analyses investigated sequences of combined monthly stream flows and the highest correlation for the Lethbridge branch growth pattern was with the combined January through May stream flow (r^2=0.79). The highest correlation for the Fort Macleod site was similarly with May stream flow (r^2 = 0.54) and analyses with multiple month data did not substantially improve the correlation fit. Spring and summer monthly stream flows were also closely correlated with the branch growth pattern at Medicine Hat and the highest coefficient of determination was obtained with combined January through March stream flow (r^2=0.66).

It is noteworthy that stream flows in the previous winter and spring were most closely correlated with branch growth increments. It might have been expected that late spring and especially, summer flows would have been more closely correlated. The correlation with earlier flows

suggests that: (i) the recharge of the riparian water table during the high flow spring period is important for subsequent cottonwood growth and (ii) cottonwood branch growth may especially occur early in the growth period.

Figure 4 demonstrates the closely correlated patterns between annual stream flows and branch growth increments at Lethbridge, Fort Macleod and Medicine Hat. However, the graphs also reveal the pseudoreplication of the present experimental design. The five sites involve the same streams flowing northeasterly from the same watersheds in the Rocky Mountains of southern Alberta and northern Montana. All of the sites experience generally similar weather and stream flow patterns and thus these do not provide independent data sets. Conversely, the close correlations between stream flow and branch growth increment does favor a causal relationship which is also founded on established physiological principles. We have subsequently studied branch growth increments along other rivers in Alberta, Montana, and Nevada and observed close correlations with environmental variables which will be described in future reports.

While a ten year record is minimal for a further conclusion, it is possible that the stream flow and branch growth correlation may especially reflect differences in growth rate across two groups of years; those with average versus those with low stream flows (Figure 5). For Lethbridge trees, growth was relatively similar in low flow years when the mean discharge was 50 $m^3 s^{-1}$ or less. During more normal flow years, branch growth was approximately doubled (Figure 4a, Figure 5). It will be useful to determine whether this possible threshold function is a product of the limited sampling interval or is typical of the branch growth response to water availability.

The period of record investigated in the present study was exceptional relative to the typical stream flows of southern Alberta. Hydrometric gauging stations on the Oldman and South Saskatchewan rivers were installed in about 1911 although the subsequent period of record is incomplete, particularly following World War II (Figure 6). The decade of branch growth record involved the lowest stream flow period on record, with stream flows through the 1980's being even lower than those during the 1930's drought (Figure 6).

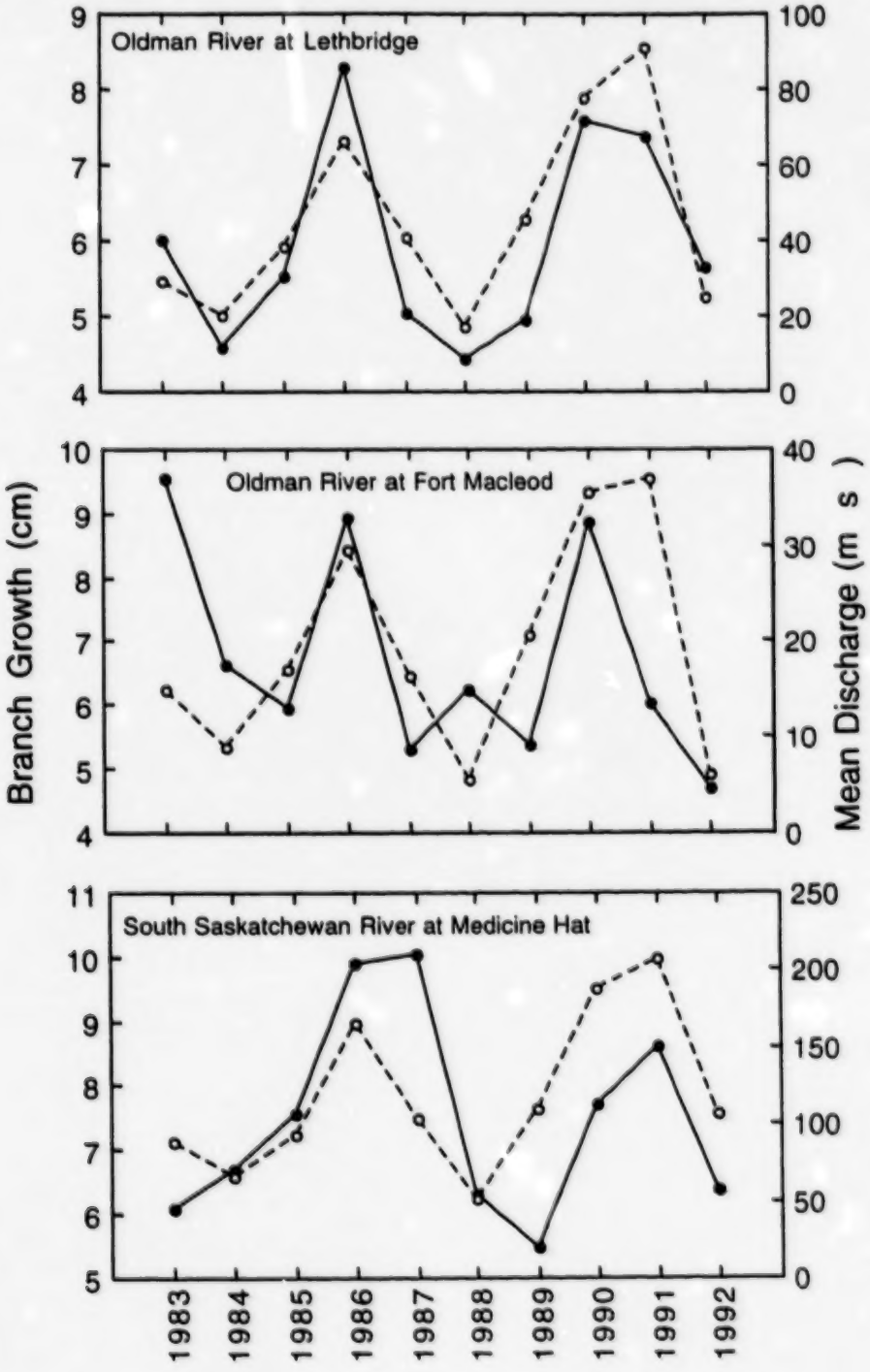


Figure 4. Annual branch growth and corresponding river discharges

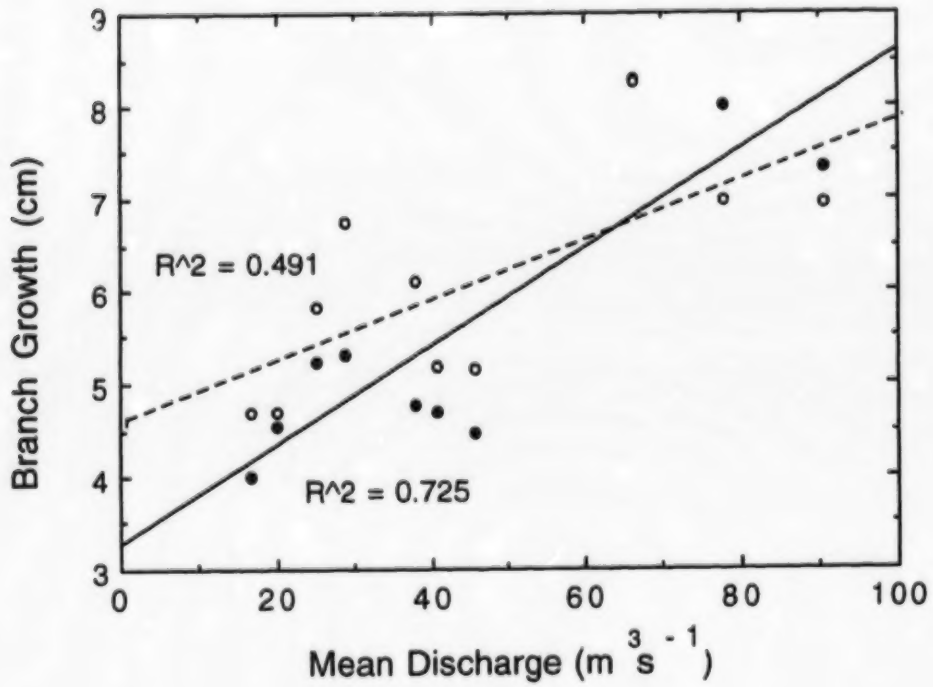


Figure 5.

Mean annual branch growth increment versus mean discharge of the Oldman River from January through May for cottonwoods in the University Grove (UG) (•) and Indian Battle Park (IBP) (o). Coefficients of determination (r^2) are included for linear regressions for the two data sets - UG: 3.2532 + 0..5374(discharge) = branch growth and IBP: 4.5959 + 0.032423 (discharge) = branch growth.

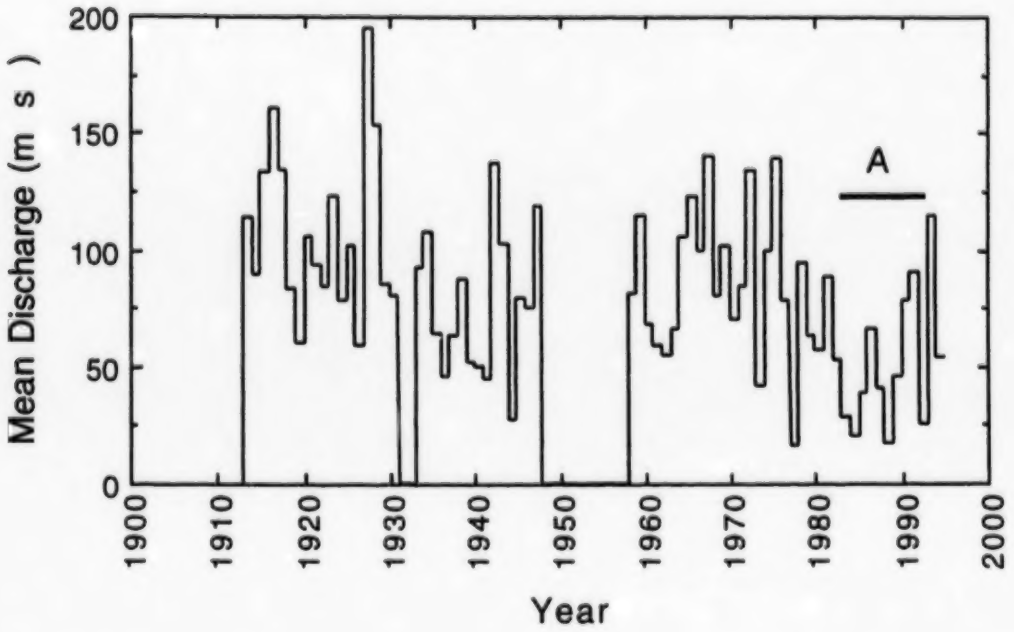


Figure 6.

Yearly mean discharge for the period of record for the Oldman River at Lethbridge, Alberta. Annual records began in 1913 but were interrupted from 1931 to 1932 and from 1948 through 1957. The period of record of branch increments analyzed for the present study (1983-1992) is designated by the solid bar below the 'A'.

The low flows of the mid- through late 1980's were due to the combination of a drought cycle and water diversion offstream for irrigation. It is probable that the low flow period created drought stress that was especially limiting for cottonwood growth. It is possible that growth would be less tightly correlated with stream flow in more normal decades during which influences of temperature and other environmental factors might contribute more substantially to the regulation of branch growth.

An alternate quantitative method for evaluating flow frequency is a return interval or recurrence analysis, which reveals the relative frequency of a flow pattern. The return intervals calculated for the decade of the present study show that only in 1991 did the flow exceed the two year return interval and no years came close to the five or ten year return interval (Table 3). This analysis further demonstrates the exceptionally low flow period associated with the present study.

Table 3.
Values and corresponding return (recurrence) intervals for maximum annual mean discharge of the Oldman River at Lethbridge (gauging station #05AD007) for the period 1981 to 1992 and estimated discharges for specific return intervals and 70 year record rank.

Year	Mean Annual Discharge (m^3/s)	Return Interval (years)	Rank in 70 year record (1 - highest, 70 - lowest)
1981	0.89	2.46	28
1982	0.53	1.28	55
1983	0.29	1.10	64
1984	0.20	1.05	67
1985	0.38	1.11	63
1986	0.66	1.57	44
1987	0.41	1.13	62
1988	0.17	1.03	68
1989	0.46	1.19	59
1990	0.78	1.73	39
1991	0.91	2.65	26
1992	0.25	1.06	66

1981 and 1982 stream flow data are included in the hydrologic analyses since it was likely that branch growth, like ring increment would be partially influenced by prior year stream flows (Stromberg and Patten 1990, and 1991). This might relate to the branch growth of 1983 that is greater than expected based on same year stream flow, particularly for Fort Macleod (Figure 4).

While branch growth patterns were best correlated with spring stream flows for all sites studied, improvements in the degree of correlation were observed with consideration for additional environmental variables. The maximizing r^2 analysis revealed that consideration of water demand as well as water supply increased the correlation fit. For the Lethbridge data, improved fit with a second step was best achieved when June pan-evaporation was considered as well as January through May stream flow (r^2=0.91). Marginally better fit (r^2=0.97) was further achieved when April stream flow was added which increased the weighting for spring rather than winter flow. For Medicine Hat, January through March stream flow provided the greatest single variable fit (r^2=0.66) and the additional consideration of July precipitation resulted in a slight improvement of fit (r^2=0.80).

A number of the climatic variables were positively or negatively correlated and these combine to influence water demand (Table 4). Warm temperatures and abundant sunshine occur in southern Alberta during periods of westerly flow, during which the powerful Chinook winds also occur. Thus, hot, dry, sunny and windy conditions are positively correlated (Table 4) and combine to produce high evaporation rates and consequently, substantial water demand from the cottonwoods and from the riparian substrate. The relatedness of weather components produces some interdependence of all of the environmental variables, including stream flow (Table 4). However, as previously noted, the Oldman and South Saskatchewan rivers through Lethbridge and Medicine Hat are exotic streams and the close correlation of branch growth with this stream flow provides strong evidence for the phreatophytic nature of cottonwoods and their dependency on the riparian water table that is closely correlated with stage of the adjacent stream rather than being dependent on local precipitation during the summer months (Rood et al. 1995).

Table 4.

Number of significant ($P < 0.05$) correlations (r) between mean monthly stream flows of the Oldman River and mean monthly weather variables for Lethbridge, Alberta for the period from 1983 to 1992, followed by number of comparisons. Correlations were positive unless noted as (-). The second lines indicate the number of significant correlations that occur in the same months for the two variables.

Variable	Stream Flow	Precipitation	Temperature	Sunshine	Wind	Evaporation
Stream flow	**6/15**	6/36	0/36	2(-)/36	2(-)/36	4(-)/36
same month:		1/6	0/6	0/6	1(-)/6	1(-)/6
Precipitation		**0/15**	4(-)/36	5(-)/36	2(-)/36	4(-)/36
same month:			2(-)/6	4(-)/6	1(-)/6	4(-)/6
Temperature			**1(-)/15**	2/36	0/36	4;1(-)/36
same month:				1/6	0/6	4/6
Sunshine				**0/15**	0/36	5/36
same month:					0/6	5/6
Wind					**4/15**	1/36
same month:						1/6
Evaporation						**1/15**

-Branch Growth versus Tree Ring Analyses-

While the present study focussed on the investigation of branch growth patterns, tree ring analyses were also conducted. Such analyses revealed some variation in annual ring increments, including some that was correlated across trees at specific sites (Table 1). However, fewer trees demonstrated correlations in ring increments than in branch growth increments at the sites studied (Table 1). The absolute sizes of radial increments were about 1/30 of the branch growth increments and the tree rings also tended to be more complacent - that is, less variation was displayed. A relatively complacent nature of cottonwood tree rings has

been previously recognized, diminishing the suitability of traditional dendrochronological analyses of cottonwood growth. Conversely, tree ring investigations have been successfully used by Stromberg and Patten (1990, 1991) to investigate impacts of stream flow diversion and determination of instream flow needs for cottonwoods along some streams.

In the present study at the Lethbridge site, some positive correlations between tree ring and branch growth increments were observed and the general patterns of variation for tree rings and branch growth were positively correlated (Figure 7, Table 2). This suggests that similar environmental variables limited cottonwood growth in the forms of both radial trunk growth and branch elongation. Conversely, at Fort Macleod there was less correlation in ring increment patterns across trees and the pattern of tree ring variation was not positively correlated with the branch growth pattern (Figure 7). The contrasting environmental limitation to radial growth in Lethbridge versus Fort Macleod might reflect differences of riparian cottonwoods in foothills versus prairie regions, with the latter being hotter and dryer. Consequently, cottonwood growth at Lethbridge would be more limited by water availability.

-Environmental Management Considerations-

The present study demonstrated the close linkage between stream flow and branch growth of riparian cottonwoods. This relationship indicates that water availability was the principal limitation for branch growth of these trees during the decade of study. It also confirms that the water source for the riparian trees is linked to the stream, consistent with the knowledge that the riparian water table is fed by stream water in these semi-arid regions. The confirmed reliance of riparian cottonwoods on adjacent stream flow emphasizes the importance of sufficient instream flows for the conservation and restoration of riparian cottonwoods.

Analyses of branch growth increments should provide a useful dendrochronological tool for determinations of instream flow needs of riparian cottonwoods and also for investigations of impacts of river damming and water diversion. Tree ring analyses have been used for similar analyses and both branch growth increments and tree rings have advantages and disadvantages. Branch growth increments are much easier to measure due to the larger size and ease of access. Measurements can be

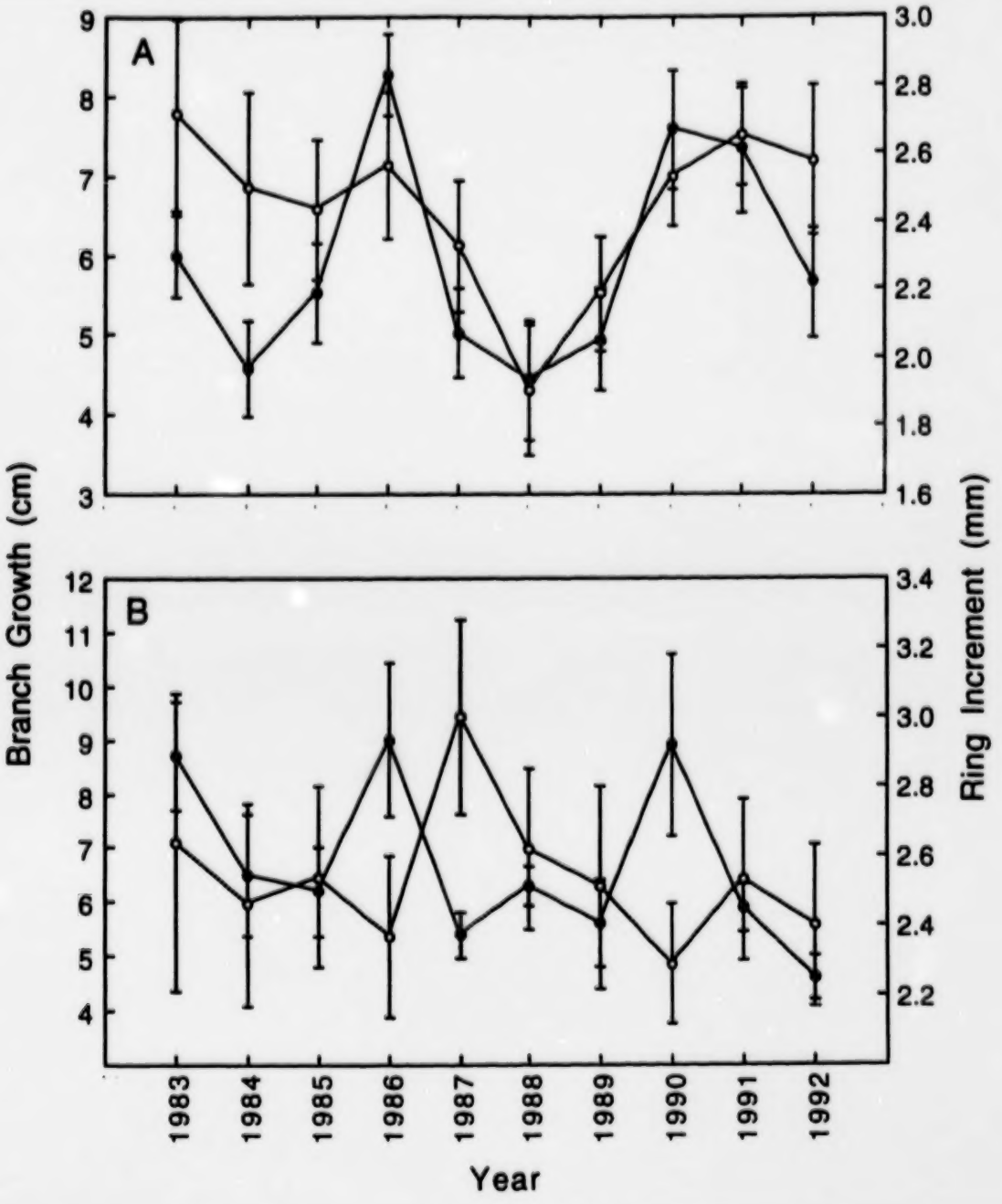


Figure 7.

1983 to 1992 annual branch growth increments (± s.e.) (•) and annual growth ring increments (± s.e.) (o) for riparian cottonwoods growing along the Oldman River at Lethbridge (top) and Fort Macleod (bottom), Alberta.

made nondestructively enabling analysis of historical branch growth increments prior to the imposition of a stream flow management pattern and subsequent monitoring of growth rates of the same branches thereafter. In the present study, branch growth increments were more consistent across trees than tree rings and also less complacent than tree rings. Conversely, while tree ring patterns may be less sensitive and less convenient, the period of record that can be studied through tree ring increments will involve a number of decades and may even reach or exceed a century. Branch growth increment analyses can usually be conducted only for the past decade although some trees allow analyses for periods exceeding two decades.

It is probably most useful to consider tree ring and branch increment analyses as complementary dendrochronological tools. Analyses of both growth patterns can provide greater confidence in interpretation of principal patterns and the two growth characteristics probably also respond to slightly different environmental and biological factors. Thus, combined analyses should increase the breadth and confidence of interpretation with respect to the influence of historical conditions on tree growth.

Acknowledgements:

This research was supported by Alberta Environmental Protection as part of the Oldman River Dam mitigation project and the South Saskatchewan River instream flows needs study. Useful discussion with John Mahoney is acknowledged as well as editorial suggestions by Lori Gom and Andrea Kalischuk.

Literature Cited:

Albertson, F. and J. Weaver. 1945. Injury and death or recovery of trees in prairie climate. Ecol. Monographs 15: 395-433.

Bradley, C.E. and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and Northern Montana. Can. J. Bot. 64. 1433-1441.

Brayshaw, T.C. 1965. The status of the black cottonwood (*Populus trichocarpa* Torrey and Gray). Can. Field Nat. 79: 91-95.

Busch, D.E., N.L. Ingraham, and S.D. Smith. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: A stable isotope study. Ecol. App. 2: 450-459.

Crouch, G.L. 1979. Changes in the vegetation complex of a cottonwood ecosystem on the South Platte River. Great Plains Agric. Council 91: 19-22.

Darrow, R.A. 1943. Vegetative and floral growth of *Fouquieria splendens*. Ecol. 24: 310-322.

Dawson, T.E. and J.R. Ehlringer. 1991. Streamside trees that do not use stream water. Nature 350: 335-337.

Eckenwalder, J. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicacae) in sections Algeiros and Tacamahaca II: Taxonomy. Can. J. Bot. 62: 325-335.

Fenner, P., W.W. Brady, and D.R. Patton. 1985. Effects of regulated flows on regeneration of Fremont Cottonwood. J. Range Manage. 38: 135-138.

Finch, D.M. and L.F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. Nat. Areas J. 13: 191-203.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London, 567 pp.

Glock, W.S. 1941. Growth rings and climate. Bot. Rev. 12: 649-713.

Herman, F.R. 1956. Growth and phenological observations of Arizona junipers. Ecol. 37: 93-

195.

Hiley, W.E. and N. Cunliffe. 1923. Further observations on the relation of the height growth of trees to meteorological conditions. Ann. App. Biol. 10: 442-452.

Hinckley, T.M., H. Richter, and P.J. Schulte. 1991. Water relations. In: Raghavendra, A.S. (ed) Physiology of trees. John Riley and Sons, Inc.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant. Physiol. 24: 519-570.

Johnson, W., R. Burgess, and W. Keammerer. 1976. Forest overstory vegetation and environment on the Missouri River Floodplain in North Dakota. Ecol. Monographs 46: 59-84.

Johnson, R.R. and L.T. Haight. 1984. Riparian problems and initiatives in the American southwest: A regional perspective. In: Warner, R.E. and K.M. Hendrix (eds) California Riparian Systems. Univ. Calif., Davis. pp: 404-412.

Kozlowski, T. 1964. Shoot growth in woody plants. Bot. Rev. 30: 335-392.

Randall, K.E. and D.T. Patten. 1991. Development of a revegetation plan for a desert riparian area in Arizona. In: Proc. 18th Ann. Conf. on Wetlands Restoration and Creation. Plant City, FL.

Reily, P.W. and W.C. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. Can. J. Bot. 60: 2410-2423.

Rood, S., J. Campbell, and T. Despins. 1986. Natural poplar hybrids from southern Alberta: I. Continuous variation for foliar characteristics. Can. J. Bot. 64: 1382-1388.

Rood, S.B. and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation. Environ. Manage. 14: 451-464.

Rood, S.B. and J.M. Mahoney. 1991. Impacts of the Oldman River Dam on riparian cottonwood forests downstream. Report to Oldman River Dam Environmental Assessment Panel, pp

Rood, S.B., J.M. Mahoney, D.E. Reid, and L. Zilm. 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. Can. J. Bot. 73: 1250-1260.

Rood, S.B. and S. Heinze-Milne. 1988. Abrupt downstream forest decline following river damming in southern Alberta. Can. J. Bot. 67: 1744-1749.

Schulman, E. 1942. Centuries-long tree indices of precipitation in the southwest (1). Bull. Amer. Meter. Soc. 23: 148-161.

Smith, S.D., J.L. Nachlinger, A.B. Wellington, C.A. Fox. 1989. Water relations of obligate riparian plants as a function of streamflow diversion on the Bishop Creek Watershed. U.S.D.A. For. Ser. Tech. Rep. PSW-110, pp 360-365.

Stromberg, J.C., and D.T. Patten. 1989. Growth dynamics of riparian species along Rush Creek, Mono County, California. Report to Los Angeles Dept. of Water and Power, pp 44.

Stromberg, J.C. and D.T. Patten. 1990. Riparian vegetation instream flow requirements: A case study from a diverted stream in the eastern Sierra Nevada, California, USA. Environ. Manage. 14: 185-194.

Stromberg, J.C. and D.T. Patten. 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo County, California. Rivers 2: 1-11.

Stromberg, J.C. and D.T. Patten. 1996. Instream flow and cottonwood growth in the eastern Sierra Nevada of California, USA. Regul. Rivers: Res. & Manage. 12: 1-12.

Tryon, E.H., J.O. Cantrell, and K.L. Carvell. 1957. Effect of precipitation and temperature on increment of yellow-poplar. For. Sci. 3: 32-44.

Tyree, M.T., K.J. Kolb, S.B. Rood, and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta: A possible factor in the decline of the ecosystem? Tree. Physiol. 14: 455-466.

3.

Cottonwood seedling recruitment along the Oldman River following the flood of 1995; by A.R. Kalischuk, J.M. Mahoney, and S.B. Rood

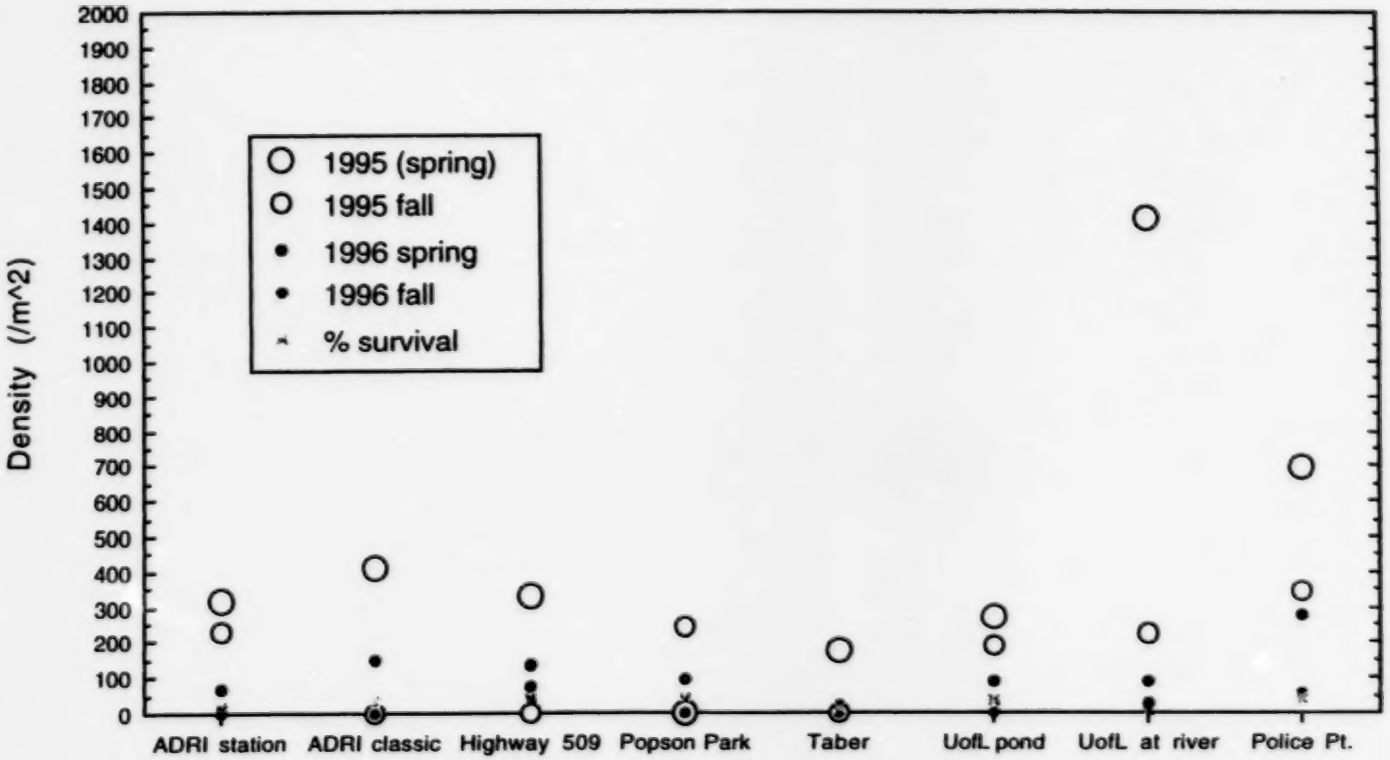
Transects extending perpendicular from the channels, with quadrats positioned along them, were established following the 1995 flood. Transects were located along a 350 km string of sites from Fernie, British Columbia, along the Elk River, across the Rocky Mountains to sites along the Castle and Upper Oldman rivers and downstream along the Oldman and subsequently, South Saskatchewan River. Most transects were permanently established with metal tags on anchor trees and positions were determined by topographic triangulation and a global position system (GPS). Transects were visited occasionally through 1995 and 1996 to investigate the establishment, survival and growth of seedlings.

This study is ongoing and will be reported more thoroughly in 1997 with continued funding having been designated from an NSERC Strategic grant associated with the conservation and restoration of riparian cottonwoods in western North America. Preliminary data are included in the following graphs which demonstrate seedling densities and heights at various locations throughout southern Alberta. Initial densities were typically about 400 seedlings per m^2 in the establishment zones along numerous transects. Densities fell by about 25% to 90% in the first summer and continued to decline through the second summer such that less than 5% of the original seedlings have survived. This still represents a massive recruitment event, since the density is still far higher than is seen in maturing woodlands.

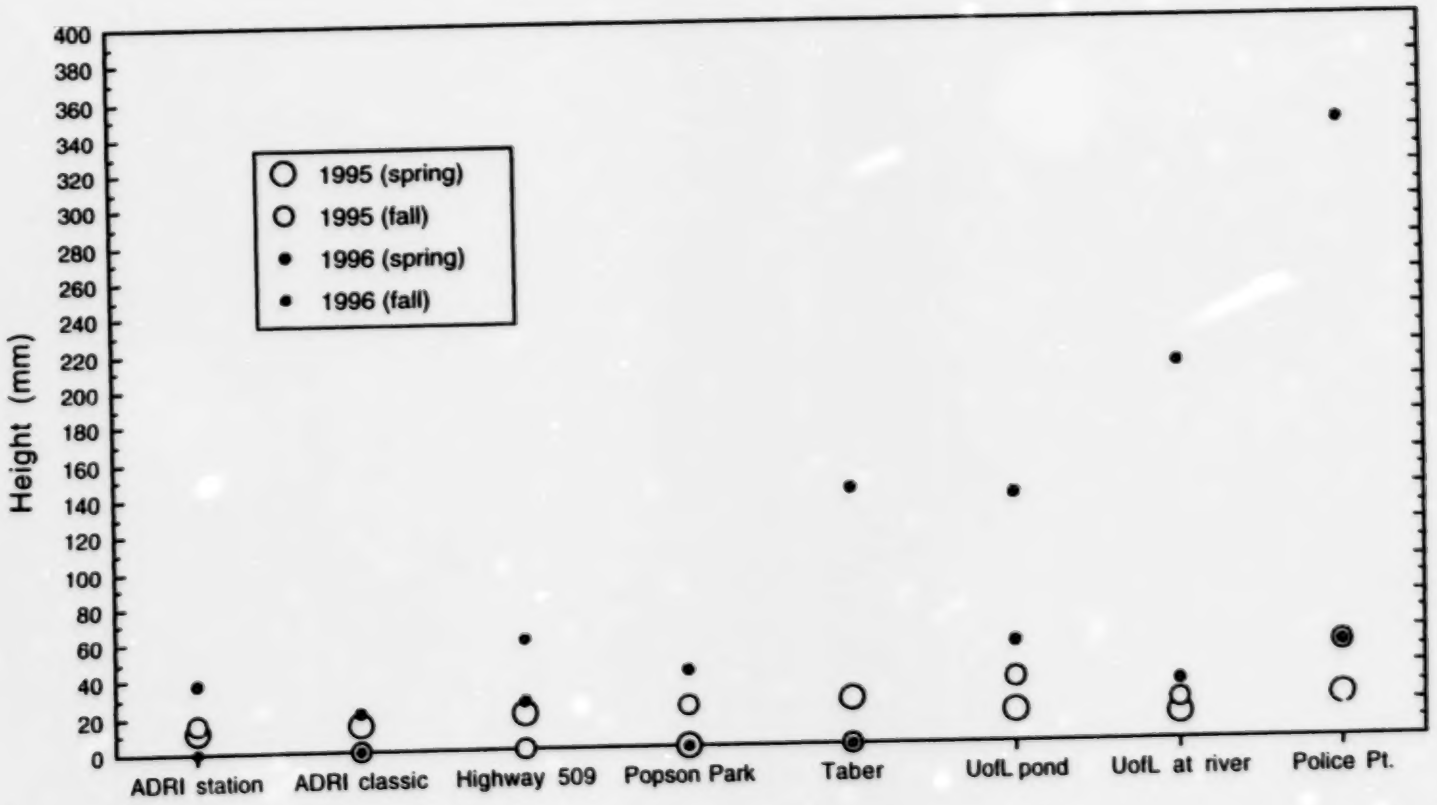
After two years of growth, seedlings are typically about 40 cm tall. Heights of over 1 m occur along the South Saskatchewan River, in the faster-growing prairie cottonwood, where the region is warmer and has a longer growing season than the foothills and mountain regions.

These figures confirm that the major 1995 flood resulted in a massive recruitment of cottonwood seedlings along the Oldman and South Saskatchewan rivers.

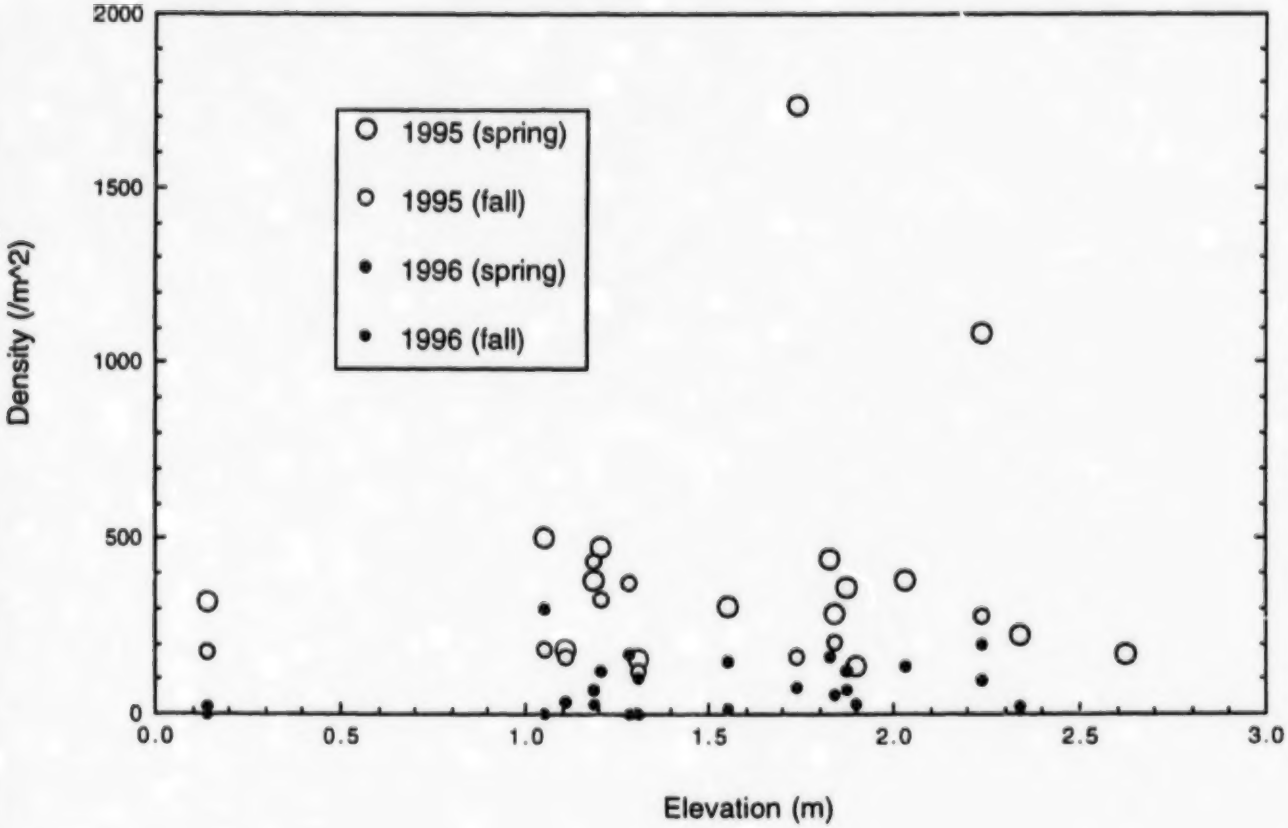
Cottonwood seedling density measurements following the flood of 1995. Percent survival is the survival after measurements in the fall of 1996 relative to initial measurements in the spring of 1995. The first seven sites (ADRI station to UofL at river) are along the Oldman river. The last site (Police Pt.) is along the South Saskatchewan river.



Cottonwood seedling height measurements following the flood of 1995. The first seven sites (ADRI station to UofL on river) are along the Oldman river. The last site (Police Pt.) is along the South Saskatchewan rive



1995 cottonwood seedling densities from seven sites along the Oldman River. 17 permantent transects were visited four times during a two year period. The elevation of the seedlings is referenced above the base flow of the Oldman River and the densities of seedlings were averaged for each quadrant at each elevation. During each visit, quadrant measurements were taken at the same location.



1995 cottonwood seedling heights from seven sites along the Oldman River. 17 permanent transects were visited four times during a two year period. The elevation of the seedlings is referenced above the base flow of the Oldman river and the heights of seedlings were averaged for each quadrant at each elevation. During each visit, quadrant measurements were taken at the same location.